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VOLUME XXXIV

THE HIPPOBOSCIDAE OR LOUSE-FLIES (DIPTERA)
OF MAMMALS AND BIRDS
PART II. TAXONOMY, EVOLUTION
AND REVISION OF AMERICAN GENERA AND SPECIES

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“Summa itaque oscitantia facillime ad colores
revocabant veteres, sed nimium ne crede colori.”

C. Linnaeus, 1751, *Philosophia Botanica*, p. 211.

INTRODUCTION

The aims and methods of this work were explained in the introduction to Part I. The preliminary sections of the present Part II discuss the taxonomy, relationships and evolution of all Hippoboscidae. They are followed by the systematic study of the American genera and species, their characters, distribution and known hosts.

The Melophaginae are not as fully treated here as the other subfamilies, the information given in my earlier “Monograph of the Melophaginae” (1942a) being condensed. That work should be consulted for additional references and records, detailed descriptions, bionomics, and copies of original descriptions. The distribution of the American species, however, is given completely by countries, states, or provinces.

One species in each genus is here figured in a complete dorsal view. Such figures are accurate enough for generic recognition, but are on too small a scale to show all specific characters. The detail drawings, keys and discussions of the affinities should be relied upon for identification.

Most figures were drawn by myself from pinned or alcoholic specimens, not from slide mounts. For the drawings of complete flies I have used also the artistic skill of Mrs. Richard O. Froeschner, Mrs. Stephen Marsh, Miss Patricia Washer, Dr. Fung Ying Cheng, Mr. Eustorgio Mendez and Dr. George Anastos, whose assistance is herewith gratefully acknowledged. In view of the many changes I have made to their work, it is not advisable to credit it to individual artists.

In the host lists of the several species, the numerals refer to the records from individual hosts I have verified personally. Names not followed by a numeral are included on the basis of published records mentioned in the bibliographies. Names preceded by an asterisk are of hosts introduced from the Old World by Man.

As the figures referring to American species in Part I are here cited again, the illustrations of Part II are numbered consecutively with those of the earlier part, starting with Fig. 22.

All persons and institutions who contributed material or information for my work are listed in a concluding section. At this

time I wish to express my special gratitude to the following colleagues who have spared neither time nor effort to assist me in many ways, particularly with regard to type specimens in their care: Mr. James E. Collin, Newmarket, England; Dr. F. I. van Emden, British Museum (Natural History); Dr. Richard Frey, Helsingfors Museum; Dr. H. Oldroyd, British Museum (Natural History); Mr. E. Séguy, Paris Museum; and Dr. Alan Stone, U. S. National Museum. To Dr. B. Lanza, in Florence, I owe valuable information on the present whereabouts and condition of some of Rondani's specimens. Dr. Fred Keiser, of the Basle Museum, was most helpful in arranging for the loan of Speiser's type of *Pseudolfersia mycetifera* from the Vienna Museum. I am under obligation to Dr. Graham B. Fairchild for recently examining several types at the British Museum.

I thank Mr. Kenneth MacArthur and the authorities of the Milwaukee Public Museum for permission to use the cuts of several illustrations previously published by the Museum from Mr. MacArthur's photographs. To Dr. Robert C. Murphy I owe the photograph of the head of *Phalacrocorax bougainvillii* infested with *Olfersia fossulata*.

The cost of reproduction of the illustrations in Part II was covered by the Museum of Comparative Zoology at Harvard College, to whom the author and the Brooklyn Entomological Society are greatly indebted.

GENERAL TAXONOMY

Historical Note. Linnaeus' genus *Hippobosca* (1758, 1, p. 607) included most Hippoboscidae he was acquainted with, except the deer-ked, which he placed among the Aptera in *Pediculus* (*Op. cit.*, p. 611). His 4 species are now referred to *Hippobosca* (*equina*), *Ornithomyia* (*avicularia*), *Stenopteryx* (*hirundinis*), and *Melophagus* (*ovina*). It is remarkable that he recognized the kinship of the sheep-ked with the louse-fly of the horse, while missing that of the deer-ked.¹ The true affinities of the deer-ked were first noted by Olivier (1792, p. 92), who described it as a new species of *Hippobosca* (*cervi*), without citing Linnaeus' *Pediculus cervi*.

No further progress was made with the taxonomy of the louse-flies until Latreille proposed (1802, 2, p. 365) to place *Hippobosca* in a special order, the Coleostoma, fully on a par with the order

¹ Massonnet's (1909, p. 13) statement that Linnaeus placed *Lipoptena cervi* in *Melophagus* was corrected later (1909, p. 228).

Diptera. But he soon modified this view (1802, **3**, p. 465; 1805, **14**, p. 397) and introduced the term "Coriacées, coriaceae" for his 98th family of Insects (his 12th family of the Diptera). This formed by itself the 2nd section of the Diptera, the remaining 11 families being the 1st section. It comprised *Hippobosca*, *Ornithomyia*, *Melophagus* and *Nycteribia*, the last-named 3 genera proposed anew, so that it was a mixture of nycteribiids and true hippoboscids. A few years later (1809, **4**, pp. 243 and 360-364) Latreille clearly recognized the nycteribiids and hippoboscids as distinct taxonomic units, the latter being his tribe "Eproboscidea" (with the family "Coriaceae") and the former his tribe "Phthiromyiae" (without family name); all remaining Diptera formed his third tribe, the Proboscidea (p. 238). At the same time he gave a surprisingly detailed and correct definition of the Coriaceae (our hippoboscids), a durable milestone in the history of the group.

The first use of the term "Pupipara" for a taxonomic concept also dates from Latreille (1817, **3**, p. 650), who proposed it to cover all the so-called pupiparous ectoparasitic Diptera known to him. It included both hippoboscids and nycteribiids, the term being exactly equivalent to his earlier "Coriaceae" (1802 and 1805). In a later edition of the same work (1829, **5**, p. 538), he reverted partly to his system of 1809, his family "Pupipara" being now divided into 2 tribes: the "Coriacés" for the known hippoboscids, but with the addition of *Strebla*; and the "Phthiromyies" for the known nycteribiids.

Leach's Omaloptera (1817, **3**, p. 60), emended to Homaloptera by Macleay (according to Westwood, 1840, **2**, p. 581), included only hippoboscids according to the original definition; but Curtis (1824, **8**) extended it to the nycteribiids also. The Hippoboscina of Newman (1834, pp. 379 and 396) included hippoboscids, nycteribiids and *Carnus*. Westwood's Thoracocephala (1840, **2**, Gen. Synopsis, p. 154, for the Hippoboscidae and Nycteribiidae), Blanchard's "Ornithomyens" (1840, **3**, p. 630), Bigot's "Cryptocères" (1852, p. 483) and "Anomalocerati" (1885, p. 226), Rondani's Hippoboscita (1875, p. 464; 1878, p. 150; 1879, p. 31), and Townsend's superfamily Hippoboscoidea (1935, **2**, p. 81) all correspond more or less to Latreille's Pupipara, but sometimes with the intrusion of extraneous elements (such as *Braula*, *Carnus*, and in the case of the Anomalocerati even parasitic Hemiptera).

Townsend (1935, **2**, p. 81) adopted the term Nymphipara for a subsection of the Diptera Schizophora comprising only his superfamily Hippoboscoidea. Presumably he followed Müggensburg

(1892, p. 292) who thought that Réaumur had used the term for a taxonomic unit, thus antedating Latreille's Coriaceae of 1802 and Pupipara of 1817. However, Réaumur (1742, 6, p. 590) merely pointed out that his so-called spider-flies (our Hippoboscidae) added a third reproductive type or class, the nymphiparous insects (cited in the French vernacular only), to the two reproductive types or classes of animals known before, namely the viviparous and the oviparous. The wording of the text shows clearly that he did not intend to propose a new taxonomic unit in the Diptera.

The use of the term Hippoboscidae in its present form for the true louse-flies seems to date from Curtis (1824, 8, letterpress to Pl. 14 of *Haemobora pallipes*, dated March 1, 1824), although he credits it to Leach in the text to Pl. 122. He applied it to one of the two families of his order Omalopectera, the other being called the Nycteribidae. A few years earlier, however, Billberg (1820, p. 123) had called "natio Hippoboscaedes" a group comprising *Hippobosca*, *Ornithomyia* and *Melophagus*. Newman's (1834, pp. 379 and 396) "natural order Hippoboscites" is another slight variant for the same concept.

The substitute Ornithomyiidae for Hippoboscidae, first introduced by E. Blanchard in the French vernacular "Ornithomyides" (1868, *Métamorphoses et Mœurs des Insectes*, p. 657) and given in the Latin form Ornithomyidae by J. Wagner (1903, *Horae Soc. Ent. Rossicae*, 36, p. 127), is very rarely used.

Family Characters. It is often difficult to draw up workable definitions of families or other higher categories, particularly among the Diptera where "annectant forms" are notoriously frequent. This is fortunately not true for the Hippoboscidae, which are one of the most sharply delimited groups of insects.

The Hippoboscidae are dorso-ventrally flattened Diptera Cyclorrhapha with many of the essential characteristics of the higher Muscoidea. The flattening is particularly pronounced for the robust head and thorax, both encased in an unusually tough, strongly sclerotized integument. The head, directed forward in a near-horizontal position, is wedge-shaped and sharply divided dorsally by the ptilinal suture into an upper vertex (consisting of postvertex, inner orbits and mediovertex) and a lower frons, both on the same plane. The frons is more or less widened, either at the upper lunula only or also over the apical interantennal portion (facial carina). The clypeus is very small, placed in the basal connecting membrane of the proboscis, beneath the apical edge of the frons. The antennae are inserted close to the oral margin, at

the sides of the frons, usually in two separate pits which are either open anteriorly or completely surrounded by a rim; exceptionally (*Ornithoica*) they occupy a single pit. Although variable in size and shape, the antennae are always flattened and modified in the same way: the first segment tends to be reduced and to fuse more or less with the sides of the lunula, being large and fully separated in *Ornithoica* only; the second segment, often but not always with a longitudinal apical slit on one side, is enlarged, sometimes in a long appendage; it is hollowed out apically into a deep cavity, which contains and hides the very small third segment bearing a short arista. Compound eyes are well developed, large or small, with many, normally shaped, small ommatidia, and separated in both sexes by a broad face. The ocelli may be large, rudimentary or absent. The maxillary palpi are usually distinct (rudimentary in *Echestypus* only), one-jointed, flattened, enclosing the haustellum at rest within their concave inner surfaces. The mouth-parts (Figs. 7A-D) are modified into a proboscis adapted to piercing the skin and sucking the blood of vertebrates: a thin, straight, needle-like haustellum comprises the closely joined labium, labrum-epipharynx and hypopharynx; it is swollen at the base into a ventral bulb and may be retracted in and protruded from a soft rostrum membrane at the under side of the head capsule; the haustellum ends in two very short labella (modified labial palpi) bearing rows of prestomal cutting teeth (Figs. 6A-B); it is moved by muscles inserted on a tentorium which comprises a hyoid. In the act of biting, the very long, slender portion of the haustellum (including most of the labium) enters the skin as far as the bulbous base. The depressed thorax is equally developed and sclerotized dorsally and ventrally; a broad sternal area extends on the sides of the median (internal) cryptosternum (characteristic of all Diptera) and separates the mid from the hind coxae, as well as the two coxae in each pair; it is much less developed between the fore coxae. The upper lateral areas (pleuro-notal sclerites) of prothorax and mesothorax are dorsal and horizontal, on a plane with the notum, the prothoracic spiracles being dorsal or dorso-lateral. A scutellum is always set off, followed by a well-developed post-scutellum, the narrow area between them (subscutellum) being usually membranous. Metathoracic spiracles are present. The robust legs, inserted at the side edges of the sternum and spread out more or less horizontally, move sideways as well as forward and backward; they end in two claws, each with a heavy basal heel and a simple or deeply cleft tip. Halteres are usually present,

except in *Melophagus*. The wings may be normal and functional or reduced in size and functionless, sometimes temporarily functional, completely rudimentary in *Melophagus* only. When most complete, the venation is essentially that of the higher Muscoidea, except for the lack of a discoidal cross-vein closing a discal cell; some of the other cross-veins and more rarely some of the longitudinalinals are missing in certain genera. The alula is present or absent. The wing membrane is often covered to some extent with microscopic hairs (microtrichia). Calypteres are either present but reduced, or absent; they never cover the halteres. The integument of the moderately flattened abdomen is mostly soft and extensible, as a rule with few or reduced dorsal sclerites (except in *Ornithoica*), ventrally with only a median basal sclerite and sometimes a pair of preanal sclerites. The male terminalia are extremely simplified, consisting at most of a pair of gonocoxites and an aedeagus of 3 rod-like pieces (2 penis valves surrounding the penis); the gonocoxites may be broad, flap-like (*Olfersia*, *Lynchia*), reduced to narrow, short, finger-shaped processes (*Ornithomyia*, *Ornithoetona*), rudimentary as minute knobs (*Ornithoica*), or absent (*Stilbometopa*). Seven pairs of abdominal spiracles have been traced in most genera and are probably present in all. The body is moderately to strongly hirsute, the bristles often long and stiff; but there are never true ctenidia of short, peg-like spines. The usual muscoid chaetotaxy is present to some extent, but often obliterated by additional setae; the head bears distinct orbital and vertical bristles. There are no functional spermathecae. Reproduction is by completely intra-uterine or adenotrophic viviparity (so-called "pupiparity"), one larva developing at a time in the uterus, where it is fed by special milk-glands. After leaving the female's body, the 3rd larval instar is motionless, takes no food and hardens the integument at once into a puparium, which opens by means of a splitting cap, as in all Cyclorrhapha, when the adult emerges. Both sexes are obligate, nearly permanent, intermittently blood-sucking ectoparasites of mammals or birds; none live on bats. The blood is stored mostly or only in the digestive tract proper, the one oesophageal diverticulum being much reduced and either wholly or partly functionless.

Other structural features, sometimes mentioned as characteristic of the Hippoboscidae, occur only in certain specialized types. They are nevertheless of sufficient interest to retain our attention, since they are found more often in this family than elsewhere. Furthermore, they point to definite evolutionary trends which

often culminate in structures functioning as extreme adaptations to permanent ectoparasitism. Indeed, there are few features of the Hippoboscidae not correlated in some way with the structure or behavior of the hosts. Massonnat (1909) first called attention to this in a detailed discussion of hippoboscid morphology, which contains many useful suggestions, although it was based only on a few Palearctic genera and species. The value of his observations is somewhat impaired, moreover, by his including for comparison the Nycteribiidae, only remotely related to the Hippoboscidae, and the Braulidae, not related with them at all.

The cover of hairs and bristles varies greatly and marked hirsuteness is not common enough to be a family character. Usually the setae or hairs are scarcely more developed than in many free-living, non-bloodsucking Diptera. In some cases (*Ornithoetona*) the thoracic dorsum is almost bare. The setae tend to be stiff and long. Hirsuteness is particularly pronounced in most subapterous and apterous flies of both birds (*Crataerina*, *Myiophthiria*) and mammals (*Melophagus*) giving them the appearance and physical properties of a burr, which helps keep the flies in the plumage or pelt. In addition, the costa of the wing remnants of the subapterous flies bears many stiff, long bristles, serving the same purpose, so that the rudimentary wings are not wholly functionless.

The structure of the head is uniform throughout the family, except for minor points, such as the relative length of frons and vertex or the extent of the postvertex. Usually a soft mediovertex occupies the middle of the face; but in *Olfersia* it is mostly obliterated by the downward extension of the sclerotized postvertex, thus increasing protection against crushing. Massonnat (1909, pp. 23-27) attempted to correlate the relative length of the head with the degree of permanency on the host. Although he used for comparison the total length (including the abdomen), a meaningless measurement in the Hippoboscidae as it varies constantly during life, his general conclusion remains true. In the fully-winged species (*Hippobosca*, *Lynchia*, *Ornithoica*, *Stilbometopa*, *Ornithoeza*, *Olfersia*, *Ornithomyia*, *Ortholfersia*, *Ornithoetona*) the head is relatively shorter (particularly as compared with the thorax) than in the subapterous and apterous forms (*Stenepteryx*, *Crataerina*, *Myiophthiria*, *Melophagus*). Moreover, in the species of *Ornithomyia* which are specific parasites of swallows (*O. biloba*, *O. fur*, *O. inocellata*) and have relatively shorter wings than usual in the genus, the head is proportionately longer than in those with a wide range of other types of hosts and with longer wings (*O. avicularia*,

O. parva, *O. fringillina*).² The head of *Allobosca*, known at present only from specimens with short wing stumps, is about as high as wide, but relatively short as compared to the thorax; this feature suggests the possibility that *Allobosca* may be fully-winged upon emergence and lose most of the membrane after reaching the host.

The compound eyes, as a rule large and mostly dorsal, always comprise many normally shaped, small ommatidia. Massonnat (1909, pp. 43-46) noted a definite correlation between the length of the wings and the size of the eyes, the subapterous and apterous species having much smaller eyes than the fully-winged forms. Thus, among the mammal-flies, in the permanently winged *Hippobosca* the eye covers $\frac{2}{3}$ of the dorsal surface of the head, in the wingless *Melophagus* only $\frac{1}{9}$, and in the temporarily winged *Lipoptena* $\frac{1}{4}$. Among the bird-flies also, the eyes are small in the subapterous *Stenopteryx*, *Crataerina* and *Myiophthiria*. As *Allobosca* has eyes as large as any of the fully-winged bird-flies, it may again be surmised that it is not truly subapterous.

The ocelli vary in a somewhat haphazard manner, but with a decided tendency to disappear. Sometimes they are so unstable that their presence or absence carries little weight as a generic or even specific character. Among the mammal-flies, 18 species in 2 genera are with, and 16 species in 6 genera without, ocelli. They are absent in nearly $\frac{2}{3}$ of the bird-flies (50 species in 7 genera) and present in slightly over $\frac{1}{3}$ (38 species in 6 genera). Furthermore, while ocelli are usually distinct in *Ornithomyia*, in some species they are small or rudimentary (*O. inocellata*); in two species they have disappeared completely, *Pseudornithomyia* being originally proposed as a genus for one of these; but both these species agree with *Ornithomyia* in every other generic character, so that I regard *Pseudornithomyia* as a subgenus only. On the other hand, *Lynchia* normally lacks ocelli; exceptionally they are more or less developed, one such species being the type of *Ornithophila*; but again this is at best a subgenus, as all other characters are those of *Lynchia*. A few other genera which I now recognize seem to differ essentially only in the presence or absence of ocelli (*Crataerina* and *Stenopteryx*; *Lipoptena* and *Echestypus*), and these too may eventually be combined.

² Massonnat's measurements of *O. avicularia* and *O. fringillina* are unreliable, as he failed to recognize these species properly and even confused *O. biloba* with *O. fringillina*.

In most hippoboscids the lower part of the frons (frontal carina of the Myiodaria) is greatly widened, flattened or slightly convex, between the antennal pits. In *Ornithoica*, however, it is restricted to a smaller upper area, below the lunula, the twin basal segments of the antennae occupying a single facial cavity and touching each other on the middle line. All other genera have the two antennae widely separated in individual antennal pits. The anterior or oral margin of the frons is either entire (straight or curved outwardly) or more or less notched and divided in lateral lobes or prongs.

The variations in size and shape of the antennae were discussed in Part I (pp. 25–27). I pointed out that a furrow is present on the 2nd antennal segment in some genera and absent in others. It is most prominent in the Ortholfersiinae, in which the cavity of the 2nd segment (enclosing the 3rd) is also more open at apex than in other hippoboscids. I described several types of antennal arista. It may be of significance that the antennae are small or very small in nearly all mammal-flies (except *Allobosca* of lemurs) and large in the bird-flies (except *Hippobosca struthionis*). In some of the latter (*Ornithoetona*, *Stilbometopa*), the 2nd segment is enlarged into a flattened, leaf-like appendage. Massonnat (1909, pp. 48–51) was unable to correlate the size of the antennae in the mammal-flies with the degree of permanency on the host. In the bird-flies, however, he thought that the antennae became longer and more bristly with increased obligate ectoparasitism, as deduced from the decreasing size of the wings. A comparison of *Ornithoetona* (with very long antennae) and *Ornithomyia* (with short antennae), both fully-winged and mobile, on the one hand, with *Stenepteryx* and *Crataerina* (with relatively short antennae), both subapterous and narrowly host-bound, on the other, scarcely supports his conclusion.

The thorax and its appendages offer the most striking changes associated with different types of hosts. Some of these were discussed in Part I (pp. 31–50) and also by Massonnat (1909, pp. 21–30 for the relative size of the thorax; pp. 56–106 for the wings and legs).

In general the dorso-ventral flattening of the thorax of the mammal-flies is less pronounced in the fully-winged forms (*Hippobosca* and Ortholfersiinae) than in those that drop the wings (*Lipoptena*, *Neolipoptena*, and *Echestypus*) or are permanently apterous (*Melophagus*). It is never as marked in these flies as in some of the bird-flies, in which, moreover, it varies considerably,

being only slight in the Ornithoicinae (*Ornithoica*), moderate in most genera of Ornithomyiinae, and extreme in *Stilbometopa* and *Olfersia*. Its development seems to be correlated with increasing body size rather than with fixity on the host (as expressed by the size of the wings) or with the type of host. In the subapterous *Crataerina* and *Myiophthiria* the thorax is not noticeably more depressed than in some of the fully-winged flies.

The meta-basisternum is sometimes produced on each side over the hind coxa as a flat, retrograde *metasternal tooth* or spur; these teeth are not correlated with the type of host. They are a generic feature of *Stilbometopa* (where they are long), *Pseudolynchia* and *Ornitheza* (where they are short); in *Lynchia* they are present in a few species, but absent in most; the other genera lack them entirely.

The relative length of the thorax is more clearly correlated with the degree of permanency on the host. In all Hippoboscidae the dorsum of the thorax is wider, as compared with its length (from the anterior margin to the hind margin of the scutellum), than in most free-living Diptera. Massonnat concluded that, in both the mammal-flies and the bird-flies, the thorax was conspicuously shorter in the subapterous and apterous species than in the more mobile, fully-winged forms. Although based on an inadequate comparison of thorax length with total body length (an unreliable measurement), his conclusion nevertheless holds. Indeed, it becomes more evident if the proportions of thorax length to thorax width are compared. Among the mammal-flies, the thorax is about as long as wide or at most $\frac{1}{4}$ wider than long in the fully-winged genera, such as *Hippobosca*, *Ortholfersia* and *Lipoptena*; whereas it is about twice as wide as long in the apterous *Melophagus*. The thorax of *Allobosca* is proportioned about as in *Lipoptena*, which again suggests that *Allobosca* is possibly not truly subapterous. Among the bird-flies the differences are even more instructive. In the fully-winged forms, such as *Ornithoica*, *Ornithomyia*, *Ornithoetona*, *Stilbometopa*, *Ornitheza*, etc., the thorax is from $\frac{1}{4}$ to $\frac{1}{3}$ wider than long; but in the subapterous *Crataerina*, *Stenepteryx* and *Myiophthiria* the thorax is only about $\frac{1}{2}$ as long in the middle as wide, or even less. This shortening is, however, counteracted in the bird-flies by the lengthening of the humeral callosities into forward projecting, pointed lobes which extend along the sides of the head. None of the mammal-flies have pointed humeral callosities, the anterior corners of the thorax being rounded off and moderately or not projecting, even in *Melophagus* where the anterior

margin of the thorax forms a rather deep inward curve. Among the bird-flies, only *Ornithoica* has the anterior margin nearly straight, with very short, scarcely projecting humeral callosities. In all the Ornithomyiinae the humeri project forward as bluntly pointed lobes; these are relatively short in the fully-winged forms, although they are much more pronounced in *Ornithoctona*, *Olfersia* and *Stilbometopa* than in *Ornithomyia*, *Ornitheza*, *Lynchia* and *Pseudolynchia*; they are unusually long and often slender in the subapterous *Crataerina*, *Stenepteryx* and *Myiophthiria*. They add greatly to the streamline shape of the flattened body and it is therefore interesting to note that they are most highly developed in the flies of swallows and swifts, a point which will be considered again later. In this connection, within the genus *Ornithomyia* the species which are strict parasites of swallows have longer and more pointed humeral callosities than those with a wide range of other bird hosts.

The size of the wings is clearly correlated with the type of preferred hosts. Among the bird-flies, the fully-winged forms use as breeding hosts less specialized types of birds; but the subapterous forms are restricted to swallows (Hirundinidae) and swifts (Apodidae), mainly aerial, fast-flying birds often nesting in colonies. The trend toward the flightless condition is more general among the mammal-flies, although the Hippoboscinae and Ortholfersiinae are fully winged and active, though slow fliers. Most other mammal-flies either have wings reduced to functionless pads (Alloboscinae of lemurs) or drop the wings upon reaching the permanent host (most Melophaginae of Artiodactyla). Finally the two species of *Melophagus*, of sheep and chamois, are completely wingless, the wings being reduced to minute rods. There is also a tendency throughout the family to reduce the venation by loss of veins, even in some fully-winged forms. It is, of course, more pronounced in the subapterous forms and even more so in the Melophaginae which use the wings only for a short time after emerging.

The legs are always well-developed and powerful. In the bird-flies they tend to become longer and more slender, particularly on the tibiae, tarsi and claws. This trend is most pronounced in the spider-like flies of swifts and swallows (*Crataerina*, *Stenepteryx* and *Myiophthiria*). Among the mammal-flies the tendency is in the opposite direction, producing the shorter and thicker legs of the Melophaginae and culminating in the greatly swollen femora and tibiae of *Allobosca*. However, this tendency is much less marked in the Ortholfersiinae and Hippoboscinae, whose legs are scarcely

shorter and thicker than those of some of the bird-flies, such as *Stilbometopa*. It is interesting to note that among the mammal-flies thicker and shorter legs are correlated with the loss or impairment of the power of flight; but the reverse is true among the bird-flies, where the subapterous forms have the longest and most slender legs.

Subfamilies and Tribes of Hippoboscidae. The Hippoboscidae are so poorly represented in the average regional fauna that little need has been felt to subdivide them above the generic level. Even on a world-wide basis they comprise in my opinion only 20 groups entitled to generic rank. A comparative study of the genera, particularly from the point of view of their possible origin and evolution, shows nevertheless that they belong to several secondary lines of descent, sufficiently distinct for recognition as subfamilies.

The only previous attempt at a supra-generic grouping, by Speiser (1908c, p. 445), recognized the subjoined five subfamilies, an arrangement adopted by Brues and Melander in their "Classification of Insects" (1932, *Bull. Mus. Comp. Zool.*, **73**, p. 347; 1954, *Op. cit.*, **108**, p. 386).

a. Olfersiinae. Hippoboscidae without ocelli, always with well-developed wings, without closed anal cell; pronotum not visible dorsally. Genera: *Ortholfersia*, *Olfersia* (now called *Lynchia*), *Icosta* (now included in *Lynchia*), *Lynchia* (now called *Pseudolynchia*), and *Pseudolfersia* (now called *Olfersia*).

b. Hippoboscinae. Hippoboscidae without ocelli, with well-developed wings, without anal cell; pronotum visible dorsally as a swelling; usually brightly colored. One genus: *Hippobosca*.

c. Alloboscinae. Hippoboscidae without ocelli, with rudimentary wings in which the posterior basal cross-vein ("Analader") is sufficiently developed and curved upward to seem to delimit an anal cell. One genus: *Allobosca*.

d. Lipopteninae. Hippoboscidae some with, others without ocelli, at most with weak wings with greatly reduced venation, the wings either dropped except for stumps or reduced to scarcely visible knobs. Genera: *Lipoptena*, *Echestypus*, and *Melophagus*.

e. Ornithomyiine. Hippoboscidae either with or without ocelli, with functional or rudimentary wings, which usually have retained the anal cell; but the species without anal cell always have ocelli and those without ocelli either have an anal cell or no longer a distinct venation. Genera: *Ornithoica*, *Ornithomyia*, *Stenopteryx*, *Ornitheza*, *Ornithoctona*, *Ornithopertha*, *Ornithophila* (now included in *Lynchia*), *Crataerina*, *Myiophthiria*, *Brachypteromyia*, and *Stilbometopa*.

My "Monograph of the Melophaginae" (1942*a*, pp. 37-38) recognized six subfamilies and I follow here the same arrangement. Only the Melophaginae were characterized thus far (*loc. cit.*). All six subfamilies are here defined on a comparative basis and their genera listed.

Only the Hippoboscinae, Alloboscinae and Lipopteninae are kept with Speiser's limits. I prefer to call the third subfamily Melophaginae, as Bezzi (1915, p. 177) suggested, deriving the name from the oldest and best known genus of the group. Speiser's Olfersiinae and Ornithomyiinae are composite groups and do not bring out the true affinities of the genera he included. Both *Ortholfersia* (placed by Speiser in Olfersiinae) and *Ornithoica* (placed by Speiser in Ornithomyiinae) are isolated genera, each of which I place in a distinct subfamily. The remainder form my subfamily Ornithomyiinae. In characterizing the subfamilies I stress the structure of frons, antennae and tarsal claws, characters not mentioned by Speiser, and attach less importance to the ocelli and venation.

1. **Ornithoicinae.** Visible area of frons restricted to the lunula and a very small, triangular, median sclerite adjoining the antennae, the twin basal antennal segments touching each other over most of their length (Fig. 24*G*). Both antennae protruding from a single facial pit; 1st segment large, completely divided from the lunula. Anterior margin of frons undivided. Thorax moderately flattened; prescutum with a nearly straight antero-dorsal margin and barely projecting, broadly rounded humeral callosities; protergum not visible dorsally; notopleuron completely separated from prescutum; basisternum of prosternum undivided (Fig. 12*B*). Tarsal claws simple, but with prominent basal heel (Fig. 24*E*). Dorsum of abdomen extensively covered by large median sclerites. In addition: ocelli present; prothoracic spiracles placed dorso-laterally on the humeral callosities; wings functional, with the complete venation of the family (three cross-veins), a well-developed alula, but rudimentary calypteres. One genus, *Ornithoica*, parasitic of birds, world-wide, with a few species (6 or 7).

2. **Ornithomyiinae.** Lunula and interantennal part of frons both well developed, the twin first antennal segments separated throughout by a flat, narrow or broad frontal carina. Each antenna protruding from its own pit (Fig. 5*A*); 1st segment small, incompletely divided from or fused with the side of the lunula. Anterior margin of frons divided into two apical lobes or prongs. Thorax (Figs. 8*A*, 9*A*, and 10*A*) much flattened; prescutum with an incurved anterior margin and distinctly projecting humeral

callosities; protergum not, or narrowly, visible dorsally; notopleuron either separated from or more or less fused with prescutum; basisternum of prosternum divided into two anterior lobes or prongs. Tarsal claws bifid, in addition to the strong basal heel which makes them appear tripartite (Fig. 12K). Median dorsal sclerites of abdomen either much reduced or mostly lacking. In addition: ocelli present, vestigial or absent; prothoracic spiracles placed dorsally; alula moderately large or rudimentary; calypteres small or rudimentary. Wings either fully developed, the venation varying with the genus, or more or less reduced in size and non-functional. The largest subfamily, world-wide, with 11 genera, all parasitic of birds.

These genera are so similar in all essential characters that they must be modifications of a single original ancestral stock. Nevertheless, one of them, *Olfersia*, is isolated from the others by the peculiar structure of the frons, warranting a further subdivision into two tribes.

2a. Tribe Ornithomyiini. Frons divided by a transverse suture or depression into an upper, broad lunula and a lower, much narrower interantennal area (Figs. 4A, D, and F, and 5A). Frons and postvertex separated by a long, soft mediovertex. The 10 genera included seem to form 3 fairly natural groups as follows:

Ornithomyia (including *Pseudornithomyia*; 12 species), *Ornithoeza* (1 or 2 species), *Crataerina* (about 7 species); *Stenepteryx* (1 species), and *Myiophthiria* (including *Brachypteromyia*; 4 species). Appendage of 2nd antennal segment short and narrow, extending little beyond the rim of the pit. Wings either fully developed and with complete venation or more or less reduced and with some of the veins or cells coalescent.

Ornithoctona (including *Ornithopertha*; 9 species) and *Stilbometopa* (5 species). Appendage of 2nd antennal segment very long and broad, leaf-like, extending much beyond the rim of the pit. Wings fully developed and with complete venation.

Lynchia (including *Icosta* and *Ornithophila*; about 30 species), *Pseudolynchia* (3 species), and *Microlynchia* (3 species). Appendage of 2nd antennal segment short and narrow, extending little beyond the rim of the pit. Wings fully developed, but with incomplete venation, lacking either the posterior basal or both basal cross-veins.

2b. Tribe Olfersiini. Frons forming one undivided sclerite, the very broad interantennal area completely fused with the lunula (Fig. 7F). Sclerotized postvertex covering most of mediovertex

to near ptilinal suture. Appendage of 2nd antennal segment short and narrow, extending little beyond the rim of the pit. Wings fully developed, with incomplete venation, lacking the posterior basal cross-vein.³ One genus, *Olfersia* (7 species).

3. **Hippoboscinae.** Interantennal portion of frons (Fig. 5B) broad, forming a flattened area completely fused with the lunula. Antennae very small, each in a deep, complete, rimmed pit; 1st segment completely fused with the side of the lunula. Anterior margin of frons deeply divided into two apical lobes. Thorax (Figs. 11C-E) moderately flattened, with a nearly straight anterior margin and broadly rounded, not projecting humeral callosities; protergum well developed, distinctly visible dorsally; notopleuron completely fused with prescutum; basisternum of prosternum undivided. Tarsal claws simple, but with prominent basal heel (Fig. 12F). Median dorsal sclerites of abdomen mostly lacking. In addition: ocelli lacking; prothoracic spiracles latero-dorsal; wings fully developed, without closed anal cell; with broad alula and distinct calypteres. One genus, *Hippobosca* (8 species), restricted to the Old World and parasitic of mammals, except for *H. struthionis* of the ostrich.

4. **Alloboscinae.** Interantennal part of frons very broad, forming a flat median area fused with the lunula (Fig. 5D). Appendage of 2nd antennal segment large, extending considerably beyond the pit; 1st segment mostly fused with the side of the lunula. Anterior margin of frons divided into two divergent lobes. Thorax moderately flattened, with a slightly incurved anterior margin and broadly rounded, moderately projecting humeral callosities; protergum very narrowly visible dorsally; notopleuron completely fused with prescutum; basisternum of prosternum undivided. Legs very short and thick; claws simple, but with prominent basal heel. Median dorsal sclerites of abdomen mostly lacking. In addition: ocelli absent; prothoracic spiracles latero-dorsal; wings reduced to short, non-functional pads with incomplete venation (Fig. 12I); no alula and no calypteres. One genus, *Allobosca* (1 species), parasitic of mammals (lemurs) and restricted to Madagascar.

5. **Ortholfersiinae.** Interantennal part of frons broad, form-

³ At one time I was inclined to place *Olfersia* in a subfamily of its own, which explains the use (at my suggestion) of the term *Olfersiinae* by de Buen (1950, p. 315). Except for the peculiar face, *Olfersia* is, however, essentially one of the *Ornithomyiinae* and to all appearances derived from the same stock.

ing a flat median area, fused with the lunula. Antennae small, partly protruding from the pits; 1st segment short, distinctly divided by a suture from the lunula; 2nd segment with a long lateral furrow, the cavity containing the 3rd segment broadly open. Anterior margin of frons very broadly emarginate, the sides produced as narrow, ridge-like prongs. Thorax moderately flattened, with a nearly straight anterior margin and broadly rounded, slightly prominent humeral callosities; protergum not visible dorsally; notopleuron completely fused with prescutum; basisternum of prosternum very broad, undivided. Legs stout; femora swollen; claws simple, but with prominent basal heel. Median dorsal sclerites of abdomen mostly lacking. In addition: ocelli absent; prothoracic spiracles latero-dorsal; wings well-developed and functional, with only two cross-veins (no closed anal cell) and with or without 2nd longitudinal vein (Figs. 14B-C); alula well-developed; calypteres rudimentary. Two genera, both parasitic of mammals (Marsupialia) and restricted to Australia: *Ortholfersia* (3 or 4 species) and *Austrolfersia* (1 species).

6. **Melophaginae.** Interantennal part of frons very broad, forming a flat median area fused or nearly fused with the lunula (Fig. 4C). Antennae small, each in a deep, rimmed pit; 1st segment completely fused with the side of the lunula. Anterior margin of frons convexly curved, entire except for a trace of a median notch at the end of a longitudinal impressed line or furrow. Thorax (Figs. 11A-B) much flattened; prescutum with a slightly incurved anterior margin and barely projecting, broadly rounded humeral callosities; protergum distinctly visible dorsally in the winged forms, fused with the prescutum in the wingless *Melophagus*; notopleuron fused with prescutum; basisternum of prosternum divided into two widely separated lobes. Legs short and thick; claws simple, but with prominent basal heel. Median dorsal sclerites of abdomen more or less developed (*Lipoptena* and *Echestypus*) or absent (*Neolipoptena* and *Melophagus*). In addition: ocelli present or absent; prothoracic spiracles placed dorsally; wings absent in *Melophagus*, temporarily present and functional in the other genera, but with greatly reduced venation; no alula and no calypteres. Nearly world-wide, with 4 genera, parasitic of mammals (Artiodactyla).

The completely apterous keds of sheep and chamois and the temporarily winged keds of goats, deer and antelopes are close relatives, as shown especially by the similarity of the frons and antennae, so that they clearly belong to one subfamily. Yet in many

respects there is a rather wide gap between the two groups, mainly owing to the presence or absence of wings, so that it seems at least convenient to place them in distinct tribes.

6a. Tribe Lipoptenini. Wings fully developed and functional in the newly-emerged adult (volant), with greatly reduced venation, breaking off beyond the hinge after the ked reaches the breeding host. Halteres present. Thorax with some of the dorsal sutures retained and with a distinct protergum. Three genera in the Old and the New World: *Neolipoptena* (1 species), *Lipoptena* (18 species; with subgenus *Lipoptenella*), and *Echestypus* (3 species).

6b. Tribe Melophagini. Wings and halteres completely aborted the wings represented by minute rods. Most of the dorsal sutures of the thorax lacking, the protergum fused with the prescutum; but the scuto-scutellar suture retained. One genus, autochthonous in the Old World: *Melophagus* (2 species; with subgenus *Dorcado-phagus*).

The foregoing arrangement in six subfamilies is based at present entirely on the external structure. In view of the general uniformity of the family both in external characters and in behavior, it seems improbable that the internal anatomy will add important characters on the subfamily level. It should be recognized, nevertheless, that this assumption is based on imperfect data. The internal anatomy is known in sufficient detail only for the sheep-ked, *Melophagus ovinus*, the most specialized member of the family, and very superficially for a few other genera, particularly *Hippobosca* and *Ornithomyia*. A general comparative study of the internal organs of the Hippoboscidae as a whole is urgently needed. It would be especially important to know whether or not the relatively primitive Ornithoicinae (*Ornithoica*) depart in this respect from the other louse-flies.

KEY TO SUBFAMILIES

1. Tip of claw divided (claw apparently trifold). Antennae each protruding from its own pit, separated by a broad or narrow frontal carina. Anterior margin of prescutum deeply curved inward, with prominent humeral callosities. On birds Ornithomyiinae
- Tip of claw simple (claw apparently bifid). Anterior margin of prescutum not or very slightly curved inward, the humeral callosities short and broadly rounded 2

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2. Both antennae protruding laterally from a single facial pit, not separated in the middle by a frontal carina. Basisternum of prosternum undivided. On birds Ornithoicinae
Antennae each in its own pit, separated by a broad frontal carina, which is more or less fused with the lunula. On mammals (except for one species on ostrich) 3
3. Antennae large, extending beyond the pits. Basisternum of prosternum undivided. Anterior margin of frons forming two divergent lobes. On lemurs Alloboscinae
Antennae small, not or scarcely protruding from the pits 4
4. Basisternum of prosternum divided into two lobes. Median dorsal sclerites of abdomen present or absent. Anterior margin of frons even, not forming two lobes. On Artiodactyla Melophaginae
Basisternum of prosternum undivided. Median dorsal sclerites of abdomen lacking. Anterior margin of frons forming two divergent lobes 5
5. Protergum well developed in front of the prescutum. Humeral callosities broadly rounded, not projecting. On Carnivora, Perissodactyla, Artiodactyla and ostrich Hippoboscinae
Protergum not visible dorsally in front of the prescutum. Humeral callosities slightly projecting forward. On marsupials Ortholfersiinae

ARTIFICIAL KEY TO HIPPOBOSCID GENERA OF THE WORLD

The purpose of the following key is to place any hippoboscid fly quickly and correctly in one of the genera I now recognize as valid. It is not intended to show relationships, these being given in a previous section on the subfamily characters.

1. Wings absent or much reduced in size and functionless 2
Wings broad, of normal shape, used for flight 9
2. Entirely without wings and without halteres. Apical tooth of claw simple (entire claw seemingly bidentate). Ocelli absent. On mammals *Melophagus*
Wings either very short, or very narrow, or reduced to basal stumps. Halteres present 3
3. Apical tooth of claw simple (entire claw seemingly bidentate).
Frons forming a single broad sclerite above and between the antennae. On mammals 4
Apical tooth of claw bifid (entire claw seemingly tridentate).
On birds 7

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4. Wings very short, but with several veins and complete cells; anal vein well developed and apparently closing an anal cell. Ocelli absent. On lemurs *Allobosca*
Wings reduced to basal stumps (broken remnants of the more complete wings of newly-emerged flies), without closed cells. On ungulates 5
5. Ocelli absent. Basal sternite of abdomen crescent-shaped, with concave hind margin. Palpi short or vestigial *Echestypus*
Ocelli present. Palpi always present, though sometimes short 6
6. Basal sternite of abdomen elliptical, with broadly rounded (convex) hind margin. Fore coxa with a dorsal retrograde spur *Neolipoptena*
Basal sternite of abdomen crescent-shaped, with deeply emarginate (concave) hind margin. Fore coxa without dorsal retrograde spur *Lipoptena*
7. Wings very short, about as broad as long, rounded at apex, scarcely extending beyond the scutellum. Eyes short. Ocelli absent *Myiophthiria*
Wings at least as long as the abdomen, drawn out into a point. Eyes long 8
8. Wings rarely over three times as long as broad, the basal portion always much wider than the abruptly narrowed apical portion. Ocelli absent *Crataerina*
Wings narrow throughout, nearly ten times as long as broad, very gradually and slightly widened basally. Ocelli present or vestigial *Stenepteryx*
9. Apical tooth of claw simple (entire claw seemingly bidentate) 10
Apical tooth of claw deeply bifid (entire claw seemingly tridentate). On birds 16
10. Wing with a closed anal cell and three cross-veins; apical portion of third longitudinal vein running close to the costa beyond 2nd longitudinal. Frons consisting mainly of the upper lunula, not extended downward between the antennae. Ocelli present. Anterior margin of prescutum seen from above nearly straight, leaving the sides of the head free. On birds *Ornithoica*
Wing without closed anal cell and with only one or two cross-veins. Frons a single broad sclerite between and above the antennae. On mammals or ostrich 11

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11. Wing with only three distinct veins behind the costa and one long, oblique cross-vein; (wings eventually breaking off near the base). On ungulates 12
Wing with five or six distinct longitudinal veins and two cross-veins; (wings retained throughout life). Ocelli absent 14
12. Ocelli absent. Basal sternite of abdomen crescent-shaped, with deeply emarginate (concave) hind margin. Palpi short or vestigial *Echestypus*
Ocelli present. Palpi always present, though sometimes short 13
13. Basal sternite of abdomen elliptical, with broadly rounded (convex) hind margin. Fore coxa with a dorsal retrograde spur *Neolipoptena*
Basal sternite of abdomen crescent-shaped, with deeply emarginate (concave) hind margin. Fore coxa without dorsal retrograde spur *Lipoptena*
14. Anterior margin of prescutum seen from above convexly rounded, without protruding humeral callosities, leaving the sides of the head completely free. Occipital margin broadly rounded. Wing with six longitudinal veins behind the costa; membrane bare, with many fine wrinkles. Not on wallabies *Hippobosca*
Anterior margin of prescutum seen from above with a slight inward curve, the humeral callosities somewhat protruding along the sides of the head. Occipital margin truncate, nearly straight. Wing membrane as a rule extensively covered with microtrichia, not wrinkled. On wallabies. 15
15. Wing with six longitudinal veins behind the costa *Ortholfersia*
Wing with five longitudinal veins behind the costa *Austrolfersia*
16. Wing with a closed anal cell and three cross-veins 17
Wing with an open anal cell and only one or two cross-veins. Wing membrane partly covered with microtrichia 22
17. Second longitudinal vein running close to the costa, the two veins partly fused beyond the apex of the first longitudinal; anterior basal cross-vein placed about midway between the anterior cross-vein and the anal cross-vein, the second basal cell much shorter than the first; wing membrane bare. Ocelli present. Antennal appendage small, narrow *Ornitheza*

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- Second longitudinal vein running over its entire length some distance from the costa, in which it ends at a distinct angle 18
18. Ocelli distinct. Anterior basal cross-vein placed closer to the anterior cross-vein than to the anal cross-vein, the two basal cells almost the same length 19
- Ocelli absent or vestigial 21
19. Antennal appendage small, narrow, without outer rim, directed outward and downward. Wing membrane partly covered with microtrichia *Ornithomyia*
- Antennal appendage broad and long, leaf-like, directed forward. Wing membrane bare or with very few microtrichia 20
20. Antennal appendage with convexly curved inner margin, narrowed apically to a blunt or sharp point, at most one-half the height of the head *Ornithoctona*
- Antennal appendage with nearly straight inner margin, with a very broad, rounded apex, about two-thirds of the height of the head *Ornithoctona* subgenus *Ornithopertha*
21. Anterior basal cross-vein placed about midway between the anterior cross-vein and the anal cross-vein, the second basal cell much shorter than the first. Antennal appendage broad and long, leaf-like. Pleurotergal process on each side of the metathorax prominent, anvil-shaped. Wing membrane without microtrichia *Stilbometopa*
- Anterior basal cross-vein placed closer to the anterior cross-vein than to the anal cross-vein, the two basal cells almost the same length. Antennal appendage small, narrow. No prominent, anvil-shaped pleurotergal processes on the metathorax. Wing membrane partly covered with microtrichia *Ornithomyia* subgenus *Pseudornithomyia*
22. Wing with only one (anterior) cross-vein; second basal and second posterior cells also combined 23
- Wing with two cross-veins; second basal cell at least partly closed 24
23. Scutellum with straight hind margin, the angular sides bearing several small, finger-shaped processes. Pleurotergal processes behind the scutellum low, scarcely developed. Ocelli absent *Pseudolynchia*
- Scutellum with convex hind margin, the rounded sides without finger-shaped processes. A prominent conical pleurotergal

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- process on each side behind the scutellum. Ocelli small, vestigial or absent *Microlynchia*
24. Interocular face about evenly divided by the ptilinal suture: the upper part is a long postvertex, sometimes with a curved transverse depression; the lower part (frons) consists of the lunula and interantennal area fused into one broad sclerite, briefly emarginate at apex. Ocelli absent *Olfersia*
- Interocular face shaped as usual: the relatively short postvertex separated from the frons by a long, soft mediovertex; lunula partly or completely divided by a suture from the much narrowed interantennal area, which ends in two slender apical arms. Ocelli usually absent, exceptionally present or vestigial *Lynchia*

GEOGRAPHICAL DISTRIBUTION

I mentioned before (Part I, p. 121) that the American bird-flies are essentially tropical insects; but this is true of all hippoboscids the world over. As shown below, this peculiarity dominates their present-day geographical distribution.

Natural Means of Dispersal. The majority of louse-flies of both birds and mammals larviposit normally away from the host (Part I, pp. 185-195), in which case the emerging flies must find a suitable host by their own means. The two species of *Melophagus*, which glue the puparium to the hairs, are exceptional. Although the deãlated females of the other Melophaginae larviposit likewise in the host's pelt, their puparia do not stick to the hairs, but drop off as a rule before emergence. Some bird-flies larviposit in nests or rookeries, where the proper host may usually be reached by running, without much trouble or hazard. This is the only method available to the subapterous bird-flies, which, moreover, are almost restricted to birds nesting in colonies used at regular intervals, where the flies may await the hosts' return or wander from deserted to occupied nests. However, the majority of fully-winged flies of mammals (Hippoboscinae and Ortholfersiinae) and of birds (Ornithoicinae and most Ornithomyiinae) must reach a proper breeding host by random flights a few hours or days after emerging and within a rather short distance from the spot of emergence (Part I, pp. 219-222).

Active dispersal to new territory is therefore very difficult for all louse-flies and their spatial distribution must depend primarily on passive transport after reaching a host. The present distribution and future extension of the range of every species of fly result

almost entirely from passive transport by effective breeding hosts. Some of the types of birds commonly parasitized by flies, such as marine swimmers, waders and diurnal and nocturnal birds of prey, often stray considerable distances beyond their normal territory, which no doubt explains the cosmopolitan distribution of some of the less specific bird-flies (*Lynchia nigra*, *L. albipennis*, and *Ornithoica confluenta*). Frigate birds (Fregatidae) are strictly speaking tropical sea-birds, but occur sometimes accidentally in temperate areas. There are records of such occurrences from eastern Canada, Germany, France and Scotland, and two of these strays carried *Olfersia spinifera* (in France, Oct. 1852: Courtiller, 1853; in Scotland, July 9, 1953: Stephen, 1953). Temporary association of a fly with an unsuitable host is a most improbable means of invading new territory, as it involves the fly's transferring to another host suitable for breeding in the new area.

Most genera and species of vertebrates occupy nowadays definite areas, often of relatively small extent, and one may expect on the whole a similar localisation for the hippoboscids. Many birds tend to spread over a wider territory than most mammals, because they are mobile and indulge in seasonal migrations which usually carry them far from the nesting sites. As a result, bird-flies are often more widely distributed than mammal-flies. In general also, flies with restricted host-specificity occupy smaller territories than those that breed on a variety of unrelated hosts. These and other points will be brought out in the following discussion.

Artificial Dispersal by Man. It was shown at some length (Part I, pp. 294-313) that the original ranges and wild hosts of most of the louse-flies of domesticated animals have been so thoroughly altered by Man, that they are now difficult to define. Except for *Hippobosca longipennis* (of Carnivora), *H. rufipes* (of antelopes), and *Pseudolynchia canariensis* (of Columbidae), these flies will be disregarded in the present discussion. Nevertheless, it is of some interest that all known louse-flies of domesticated animals originated in the Old World, an obvious corollary of the Old World origin of the domesticated hosts.

Dispersal by Man is not necessarily limited to the further diffusion of domesticated hosts. Louse-flies are spread sometimes to new territory in attempts to acclimatize wild hosts. Following the importation of infested deer, the European deer-ked, *Lipoptena cervi*, became permanently established on native deer (*Odocoileus virginianus*) in the northeastern United States within the past 50 to 75 years. I regard the occurrence of the American

Ornithoica vicina in the Hawaiian Islands as due to the agency of Man (1941b, p. 289), and I explain on the same basis the presence of the Holarctic *Ornithomyia fringillina* in New Zealand and Australia. In these areas foreign birds have been introduced on a larger scale than anywhere else (see G. R. Williams, 1953, *The Ibis*, 95, pp. 676-692).

Until the advent of aviation some 50 years ago, obligate ectoparasites could be imported by Man only by transport on live hosts. The extraordinary speed with which aircraft now connects distant parts of the world, has resulted in a novel and most effective method of bringing a variety of insects to new areas. Hippoboscidae are occasionally intercepted on planes arriving from foreign countries, in spite of the specialized habitat and relative scarcity of these flies.⁴ I recorded (1951) *Pseudolynchia canariensis*, *Hippobosca variegata* and *Olfersia aenescens* being found under such circumstances in North America and the Pacific area and called attention to earlier records by Whitfield (1939, p. 51) of *Hippobosca variegata* (= *maculata*) and *H. camelina* being taken on aircraft landing at Khartoum. Hughes (1949, p. 32) had previously listed the following hippoboscids among the insects found from July 1, 1944, to June 30, 1945, on planes arriving from abroad at eastern United States airports (Brownsville, Fort Worth, New Orleans and Miami) and in Puerto Rico: *Lynchia* sp. (1 dead); *Ornithoica* sp. (1 dead); *Pseudolynchia canariensis* (2 dead and 2 alive); and 1 dead undetermined fly. Thompson (1952a) observed a *Hippobosca variegata* alive on the window in a plane shortly after leaving El Adem, Anglo-Egyptian Sudan, September 22, 1950. Dr. J. H. Hughes informs me (*in litt.*, 1953) that the collection of the Division of Foreign Quarantine of the U. S. Public Health Service contains a specimen of *Olfersia fossulata* taken February 19, 1949, on a plane arriving at New Orleans from Balboa, Panama. I have also seen at the U. S. National Museum a female *Hippobosca camelina* found dead on a plane landing at New York, June 2, 1947, from Buenos Aires, after stopping *en route* in Puerto Rico. As *H. camelina* is a strictly Old World fly, it could have

⁴ These occurrences are perhaps less surprising in view of the large numbers of arthropods that now travel continuously on aircraft the world over. Hughes (1949) reports that during the 10-year period 1937-1947, of 80,716 planes inspected at United States airports upon arrival from abroad 28,752, or 35.6 per cent, carried arthropods. Of 106,106 arthropods intercepted, 16,846 were alive.

entered the plane only on a previous flight to Africa. The possibility that species of Hippoboscidae may be temporarily imported or even become permanently established after escaping from aircraft, will have to be considered in the future in appraising unusual occurrences.

General Distribution. Three of the six subfamilies, the Ornithoicinae, Ornithomyiinae and Melophaginae, are cosmopolitan, the others being restricted to the Old World. Among the latter, the Hippoboscinae are at present widely distributed on domesticated animals in Europe, Africa, Madagascar, southern Asia (as far north as Peking), Indonesia, New Caledonia, and recently Australia; but they are known on wild hosts in Africa and Arabia only, which area was probably their original, natural habitat before Man interfered. The Alloboscinae are restricted to Madagascar and the Ortholfersiinae to Australia and Tasmania.

Of the 20 genera here recognized as valid, 9 occur on original wild hosts in both the Western and Eastern Hemispheres: *Ornithoica*, *Ornithomyia*, *Crataerina*, *Myiophthiria*, *Ornithoctona*, *Lynchia*, *Pseudolynchia*, *Olfersia*, and *Lipoptena*; 8 are precinctive in the Old World: *Ornitheza*, *Stenopteryx*, *Echestypus*, *Melophagus*, *Hippobosca*, *Allobosca*, *Ortholfersia*, and *Austrolfersia*; and 3 are peculiar to the New World: *Stilbometopa*, *Microlynchia*, and *Neolipoptena*. The New World is therefore somewhat poorer in generic types than the Old, besides lacking peculiar subfamilies. The relative wealth in hippoboscids of the Old World is even more striking on the specific level, as it has 87 to 89 native species, as compared with 43 in the New World, only 8 of these occurring in both areas.

Factors Regulating Specific Distribution. The spatial distribution of integral ectoparasites, such as the Hippoboscidae, is irrevocably tied up with the presence or absence of appropriate hosts. The discussion of the host-parasite relation in Part I stressed throughout that, whatever happens to individual flies, the only normal or true hosts from the point of view of the species are those on which it can maintain itself through successive generations, or what I called the breeding hosts (Part I, pp. 218-219). I have also shown that the degree of specificity varies within the family from flies restricted to one or a few species in one genus of hosts to such with multiple suitable hosts sometimes belonging to several unrelated orders. Host specificity is more pronounced for the mammal-flies than for the bird-flies and it is, on the whole, ecological rather than taxonomic (Part I, pp. 332-336). These and some other

minor peculiarities of hippoboscid specificity have an important bearing on the past and present-day geographical distribution of the flies.

While a given species of hippoboscid obviously cannot occur in the absence of a suitable host, the presence of such a host does not necessarily imply that of its specific louse-fly also. The distributions of host and parasite do not always coincide, as is sometimes assumed or even claimed. Macroclimatic and possibly other factors outside the host are by no means negligible (Part I, pp. 120-124). Indeed climate, not the lack of appropriate breeding hosts, usually checks the northward extension of louse-flies. This is well illustrated by *Lipoptena mazamae*, a common and widespread parasite of Cervidae in tropical America, where it flourishes on several species and races of two genera (*Mazama* and *Odocoileus*). It enters temperate North America in the southeastern United States, extending as far north as South Carolina along the Atlantic coast (to about 33° 30' N.), where it occurs on Virginia deer (*Odocoileus virginianus*). North of this latitude, however, and throughout the northeastern United States and eastern Canada lies a vast area where Virginia deer harbor no autochthonous deer-keds.⁵ In the passage cited above I have presented further evidence of the influence of the macroclimate on louse-fly distribution.

Specific Types of Distribution. In view of the foregoing considerations, it is not surprising that the distribution of the hippoboscids does not fit well in the customary frame of the Earth's zoogeographical realms, regions, subregions and provinces. It seems more profitable to analyze the several types of distribution observed among these insects. As explained before, most of the flies that owe their present distribution at least in part to the agency of Man will not be included in the following discussion. *Hippobosca longipennis*, *H. rufipes*, *Pseudolynchia canariensis*, and *Lipoptena cervi* are considered only in so far as they have been found on autochthonous wild breeding hosts.

1. Not more than 7 species are nearly ubiquitous or cosmopolitan, having spread by natural means to both the Western and the Eastern Hemispheres. Three species of *Olfersia* live on oceanic birds, the genera and sometimes even the species of their hosts oc-

⁵ The present occurrence of the European deer-ked, *L. cervi*, on Virginia deer in a few localities in New Hampshire, Massachusetts, New York and Pennsylvania does not detract from this statement, as this parasite is a recent introduction by Man.

curing over all oceans: *O. spinifera* of frigate birds; *O. aenescens* of various swimmers, but chiefly boobies and tropic-birds; and *O. fossulata* mainly of guanays, pelicans and boobies. Three other flies parasitize continental birds: *Ornithoica confluenta* and *Lynchia albipennis* of waders (Ciconiiformes), and *Lynchia nigra* of birds of prey (Falconiformes and Strigiformes). As shown by the details of their distribution, the foregoing six flies are tropicopolitan rather than cosmopolitan; they are most common in the Tropical Zone, beyond which they extend only over limited areas or as sporadic strays with the accidental wanderings of the hosts. The seventh species, *Olfersia fumipennis*, a specific parasite of the osprey (*Pandion*), is more widespread than the others and in fact the most nearly cosmopolitan hippoboscoid. It is known in the Old World from Finland (close to 63° N.) to Indonesia and in the New World, from British Columbia (close to 51° N.) to Rio de Janeiro, but will probably be found wherever ospreys nest, near the sea as well as far inland.

2. The distribution of the one strictly Holarctic hippoboscoid, *Ornithomyia fringillina*, will be considered in detail in the taxonomic section. It is definitely known in Europe and northern Asia from the Shetlands, Iceland, northern Scandinavia, and Finland (close to 70° N.) to northern Italy, northern China and Japan; but the data for its distribution in Asia are inadequate. There are, however, no reliable records from Africa, Asia Minor, southern Asia, and Indonesia. Flies indistinguishable from *fringillina* occur in Australia and New Zealand; but I regard this as due to recent importations by Man of infested European birds. In America it extends from Alaska and the Yukon in the west (68° N.) and Labrador in the east (53° 20' N.) to Mexico City; but the 5 and only records from south of the Rio Grande were possibly stray flies brought in by migrant hosts from farther north. As noted before (1950, p. 113; Part I, pp. 121-122), *O. fringillina* is the hippoboscoid which has spread farthest north.⁶ Of the 7 arctic or subarctic New World records, 2 are from typically boreal birds, the hawk owl (*Surnia ulula*) and the pipit (*Anthus spinoletta*), which occur also in the northern Palearctic Region. All evidence points to *fringillina* being autochthonous in North America. It is the only

⁶ The statement in Part I (p. 124) that the sheep-ked is the hippoboscoid which reaches farthest north is erroneous, as it does not extend nearly as far as *O. fringillina*; moreover, its present northern distribution is artificial and due to importation by Man.

louse-fly for which direct arrival on hosts crossing Bering Strait, after the last Glacial Period, may be postulated.

3. The Palearctic Region has some 10 preinictive species. Six of these occur on mammals: *Melophagus rupicaprinus* and *Lipoptena couturieri* of chamois; *L. cervi* of roebuck and red deer; *L. japonica* of dwarf serow; and the poorly known Siberian *Lipoptena moschi* of musk-deer and *L. antilopes* of zeren. Four bird-flies are probably also restricted to this area, although it is as yet unclear whether all are specifically distinct from tropical forms: *Ornithomyia biloba* and *Stenopteryx hirundinis* of swallows; and *Crataerina pallida* and *C. propinqua* of swifts.

4. There appear to be only 5 strictly Nearctic flies, 2 on mammals (*Lipoptena depressa* and *Neolipoptena ferrisi* on deer) and 3 on birds (*Lynchia hirsuta* and *Stilbometopa impressa* on quail and related game birds, and *Myiophthiria fimbriata* on swifts).

No species of hippoboscids restricted to the temperate zone of the Southern Hemisphere (south of the Tropic of Capricorn) is known to occur at the same time in the Old and the New World.

5. Only one fly, *Ornithomyia parva*, is definitely peculiar to the temperate part of South America (at least to 40° 20' S.). It is mainly a parasite of various Passeriformes, although breeding also regularly on two flightless rails, and appears to be the southern representative species of the Holarctic *O. fringillina*, which has similar host preferences. *O. parva* is of more than passing interest as the only hippoboscids of the few endemic land birds of the Tristan da Cunha Group, which lies in mid-Atlantic and actually closer to Africa than to America. *Lynchia penelopes* Weyenbergh (1881), described from Argentina, is at present unrecognized and must be omitted from this discussion.

6. The hippoboscids fauna of the temperate southern half of Australia and Tasmania is inadequately known, so that the following remarks are provisional. I have recognized some 16 native species in several collections seen in recent years; but about half of them are widely distributed in the Paleotropics or extend at least to northern Queensland, New Guinea or Indonesia. The 4 or 5 species of wallaby-flies (*Ortholfersia* and *Austrolfersia*) are, so far as known, restricted to temperate Australia and Tasmania. Among the bird flies, *Ornithomyia fuscipennis* Bigot (= *O. perfuga* Speiser), 2 presumably undescribed species of *Ornithomyia* of swallows, and one species of *Lynchia* are possibly also preinictive.

New Zealand harbors at present only 3 hippoboscids, all widespread species and, I suspect, introduced by Man during the past two centuries.

7. The Paletropical Realm is richer in hippoboscids than any other similar main division of the earth, even though it is as yet far from sufficiently explored. Of the 68 or more species known from that area, 7 are cosmopolitan, 12 occur also in the Palearctic Region or extend into the temperate part of Australia, and the remaining 49 are tropical endemics. The western and eastern Paletropics, as divided by the Indian Ocean, show such sharp faunal differences, particularly in regard to mammals and birds, that they should be considered separately. Indeed, they have no tropical endemics in common. The following 18 or 19 species are restricted to the Ethiopian Region (continental Africa and southwestern Arabia): *Hippobosca fusca*, *H. hirsuta*, *H. longipennis* (on wild hosts), *H. rufipes*, *Lipoptena hopkinsi*, *L. chalcomelaena*, *Echestypus binoculus*, *E. paradoxus*, and *E. sepiaceus* of mammals; *Hippobosca struthionis*, *Ornithomyia fur*, *O. inocellata*, *Crataerina acutipennis*, *Ornithoctona laticornis*, *Lynchia pilosa*, *L. schoutedeni*, and 3 or 4 undescribed *Lynchia* on birds. The Oriental Region (from India to Formosa, the Fijis and Queensland) has 30 preinictive species as follows: *Lipoptena efovea*, *L. grahami*, *L. pauciseta*, *L. rusaecola*, and *L. gracilis* on mammals; *Ornithoica pusilla*, *O. unicolor*, *O. philippinensis*, *Ornithomyia comosa*, *Ornithoctona australasiae*, *O. plicata*, *O. soror*, *Crataerina longipennis*, *Myiophthiria lygaeoides*, *M. reduvioides*, *Lynchia acromialis*, *L. chalcopampa*, *L. dioxyrhina*, *L. longipalpis*, *L. nigrita*, *L. papuana*, *L. parallelifrons*, *L. bicorna*, *L. samoana*, *L. suvaensis*, *L. sarta*, *L. trita*, *L. tuberculata*, *L. vagans*, and *L. simplex* on birds. The eastern section thus proves to be richer in bird-flies and poorer in mammal-flies than the western section.

In the foregoing paragraph the African continent has been treated as a unit. Although there is a slight decrease in the number of species both north of the Tropic of Cancer and south of the Tropic of Capricorn, the hippoboscid faunae of these more temperate or subtropical areas differ little from that of the strictly tropical part and it is difficult to draw the line between them.

Few hippoboscids are known from Madagascar, the Mascarenes and the neighboring islands in the western Indian Ocean, no doubt owing to insufficient collecting. Neglecting the introduced *Hippobosca variegata* of cattle and *Pseudolynchia canariensis* of domestic pigeon, only 6 or 7 species have been recorded. One is a preinictive mammal-fly, *Allobosca crassipes* of lemurs. The others are bird-flies widespread elsewhere: *Lynchia albipennis* and *Ornithoica confluenta* are cosmopolitan; *Pseudolynchia rufipes* (originally described from Reunion) occurs throughout Africa,

the Oriental Region as far as the Philippines, and occasionally in southern Europe; *Ornithoetona laticornis* (= *Ornithoetona idonea* Falcoz, described from Madagascar) is Ethiopian; and *O. plicata* is common throughout the Oriental-Indonesian Region as far as Queensland and Samoa. Falcoz (1930, p. 47) records *Lynchia dioxyrhina*, originally described from New Guinea, from Great Comoro I., but this will need confirmation.⁷ The Hippoboscidae contribute nothing of importance to the problem of the Ethiopian or Oriental ("Gondwanian") origin of the Malagasy fauna.

The fair-sized Hawaiian Islands, in mid-Pacific over 2000 miles from California, 3000 miles from Japan and 4000 miles from Australia, have a highly peculiar fauna. It is perhaps more noteworthy for its negative than for its positive features and has been the subject of much controversy. The 8 species of Hippoboscidae throw no light on the matter. Two of them, the sheep-keed and the pigeon-fly, were introduced by Man with domestic animals. Two are cosmopolitan flies of oceanic birds: *Olfersia spinifera* and *O. aenescens*. *Lynchia nigra*, a cosmopolitan parasite of birds of prey, occurs on the native, endemic owl, *Asio flammeus sandwichensis*. *Ornithoica pusilla*, common on a variety of hosts in Indonesia, Australia and the Pacific Islands, has been taken in Hawaii on the endemic owl, on a parrot introduced from Australia (*Melopsittacus undulatus*) and on 2 honey creepers (Drepanidae), a family of birds precinctive of the Islands. *Ornithoica vicina*, of the New World, taken only on introduced pheasant, white-eye (*Zosterops*), and English sparrow, is clearly a recent importation by Man. The fly which Speiser (1902c, p. 89) reported from Molokai as *Ornithomyia varipes* and which I doubtfully referred (1941b, p. 260) to *Ornithoza metallica*, was actually *Ornithoetona fusciventris*, a common New World species; it may also be a recent human importation. This medley clearly consists of accidental waifs which, in so far as they are truly autochthonous, reached the Islands from time to time on stray birds.

8. Some of the common and therefore most characteristic hippoboscids of the Paleotropical Realm, are not strictly precinctive

⁷ *Ornithomyia variegata* Bigot, described from New Zealand, is, to judge from the type, a synonym of *O. fringillina*. Speiser (1908a, p. 178; 1908b, p. 204; 1908c, p. 308) recorded *O. variegata* from Madagascar, but without further data. *Olfersia testacea* Macquart, described from Reunion, is the pigeon-fly, *Pseudolynchia canariensis*.

but extend either normally or casually to the temperate zones, especially in the southern Palearctic Region. The following 7 bird-flies belong in this group: *Ornithoica turdi*, *Ornithomyia avicularia*, *Crataerina melbae*, *C. obtusipennis*, *Pseudolynchia canariensis* (on wild hosts), *P. rufipes*, and *Ornithoeza metallica*. The most interesting is *Ornithomyia avicularia*, which has spread farther north than any and is a normal element of the Palearctic fauna. In Europe it does not occur as far north as *O. fringillina*, stopping at the Shetlands, southern Scandinavia and southern Finland, and is much scarcer in these northern areas than *fringillina*. It seems to be widespread in the Old World tropics, as I have seen it, in Africa, from Uganda, Tanganyika Territory, Ruanda and the Belgian Congo, and, in the Oriental area, from Ceylon, Tonkin, Formosa, the Philippines, Australia, Tasmania, New Caledonia and New Zealand (? introduced here). The unusually wide range of this fly is no doubt due to its low grade of host specificity (Part I, p. 327). For instance, in the British Isles alone Thompson (1954a, pp. 31-33) reports it from 46 species of Passeriformes, Piciformes, Cuculiformes, Strigiformes, Falconiformes, Ciconiiformes, Gruiformes, Charadriiformes, Columbiformes and Galliformes, an impressive list, even though it includes casual in addition to effective breeding hosts.

9. The Neotropical Realm is much poorer in hippoboscids than the Paletropics, even though its fauna is more thoroughly explored, so that the relative poverty will only be enhanced by future research. The number of strictly precinctive species is further reduced by the greater tendency of the flies to move into temperate and subtropical areas. Out of a total of 36 species known to occur in the Neotropics, 7 are cosmopolitan and 15 extend north of the Tropic of Cancer or south of the Tropic of Capricorn. This leaves only 14 species restricted to the Neotropical Realm, or less than half of the total: one mammal-fly, *Lipoptena guimarãesi*; and 14 bird-flies, *Ornithomyia ambigua*, *O. hoffmannae*, *Ornithoctona oxycera*, *O. orizabae*, *O. nitens*, *Stilbometopa legtersi*, *S. ramphastonis*, *Myiophthiria neotropica*, *Lynchia latifacies*, *L. plaumanni*, *Microlynchia crypturelli*, *M. furtiva*, and *Olfersia coriacea*.

The Antilles, excluding Trinidad, Tobago and the islands off the Venezuelan coast, have only a depauperate tropical American hippoboscid fauna, without distinctive features. There are no mammal-flies, owing to the lack not only of Cervidae (the only autochthonous mammalian fly hosts in the New World) but of all Artiodactyla. The 15 Antillean bird-flies comprise all 7 known

cosmopolitan species, *Ornithoica confluenta*, *Lynchia nigra*, *L. albipennis*, *Olfersia fumipennis*, *O. spinifera*, *O. aenescens*, and *O. fossulata*; 7 flies widespread in the New World, *Ornithoica vicina*, *Ornithoictona erythrocephala*, *O. fusciventris*, *Stilbometopa ramphastonis*, *Pseudolynchia brunnea*, *Microlynchia pusilla*, and *Olfersia sordida*; and the apparently preinictive *Stilbometopa fulvifrons* (except for one stray New Jersey record). The last-named belongs, however, to a genus as yet imperfectly known; it may eventually be found on the South American continent also. That the Hippoboscidae of the Antilles are a commonplace lot is to be expected, as the area is the bridge commonly used by many migratory birds travelling back and forth between North and South America.

10. As mentioned in the discussion of the Neotropical flies, the Nearctic Region shares many of its hippoboscids (14 species in all) with Central and South America. Only one of these is a mammal-fly, *Lipoptena mazamae*, briefly considered in a previous discussion of the factors regulating distribution. The remaining 13 are bird-flies: *Ornithoica vicina*, *Ornithoictona erythrocephala*, *O. fusciventris*, *Stilbometopa fulvifrons*, *S. podopostyla*, *Lynchia americana*, *L. angustifrons*, *L. holoptera*, *L. wolcottii*, *Pseudolynchia brunnea*, *Microlynchia pusilla*, *Olfersia sordida*, and *O. bisulcata*. To these must be added 5 of the cosmopolitan flies listed under 1 (except *Olfersia aenescens* and *O. fossulata*) and the Holarctic *Ornithomyia fringillina*.

11. Apart from the preinictive *Ornithomyia parva* discussed before and the cosmopolitan *Lynchia nigra* and *L. albipennis*, the 9 hippoboscids recognized at present in the temperate part of South America (south of the Tropic of Capricorn) are all species that invade the area from the Neotropics. Most of these occur only in the northern, more subtropical sections, but a few do reach northern Patagonia. Unfortunately information on this vast area is scant and some of it does not seem fully trustworthy. At present there are reliable records for one mammal-fly, *Lipoptena mazamae* (to 27° 30' S.) and 8 bird-flies: *Ornithoica vicina* (to Puerto Montt, Chile, 41° 30' S., the southmost for any New World hippoboscid), *Stilbometopa legtersi* (to about 25° S.), *Crataerina seguyi* (to about 32° 30' S.), *Ornithoictona erythrocephala* (to about 33° S.), *O. fusciventris* (to about 28° S.), *Lynchia americana* (to about 28° 30' S.), *Pseudolynchia brunnea* (to about 38° S.), and *Microlynchia pusilla* (to about 25° 20' S.). Only two of these (*C. seguyi* and *S. legtersi*) are additional to the list of flies entering the Nearctic Region from the tropics.

Conclusions. Some fifty years ago Speiser (1908c) published an essay on the geographical distribution of the Hippoboscidae (and other ectoparasitic pupipara), intended to correlate it with their phylogeny. This creditable review of the contemporary knowledge of the flies contained some valuable suggestions, but did not throw much light on the phylogeny of the family. The foregoing review shows that the distributional pattern of the Recent Hippoboscidae is extremely complex, controlled as it is at present by the interaction of different types of host specificity, ecological peculiarities of the hosts (particularly their seasonal migrations) and macroclimatic factors. All three influences were active also throughout the geological past with continually varying and mostly unknown results, so that it is difficult to see how the present-day distribution of the flies could teach much about their past history.

It is most unlikely that the fossil record will ever furnish adequate pertinent data, particularly owing to the difficulty of determining the true host relations of extinct flies. When the fossil fits in a Recent genus, as in the case of *Lynchia rottensis*, it may be safe enough to decide whether it was a bird-fly or a mammal-fly;⁸ but to go beyond this is blind guesswork. If, however, some fossil fly were discovered so aberrant that it could not be placed in any Recent genus or subfamily, it would be utterly impossible to settle the type of vertebrate on which it lived.

Another consideration should warn us to be most cautious in drawing conclusions from the present-day distribution of the louse-flies. It will be generally agreed, I suppose, that no appreciable addition has been made to the sum total of living animal genera and species since the start of the Holocene or Recent Era, but that on the contrary there has been a steady loss. In some groups of animals this loss possibly does not affect appreciably the validity of conclusions based on what remains available for study to-day. In the case of the Hippoboscidae, however, it is of unusual importance, first because of the very limited number of Recent genera (20) and species (fewer than 150 known at present), and second because of the fairly strict host specificity of most flies. Ever since the dawn of Man the destruction of the vertebrates has been carried on with increasing vigor and it has particularly gained momentum during the past 500 years. The list of the known extinct Recent mammals and birds is now extensive and some of them

⁸ The Recent *Hippobosca struthionis*, a bird-fly of a genus otherwise restricted to mammals, shows that even this type of evidence is not always conclusive.

were no doubt potential hosts of louse-flies. As a result, it is no longer possible to determine what the original Recent fauna of louse-flies and their hosts may have been at the close of the Pleistocene in the Mediterranean countries, western Europe, much of the United States and South Africa. Under the circumstances it seems futile to attempt to trace from the present-day distribution the possible routes of migration of the living Hippoboscidae.

The remarks to follow will be more in the nature of a summary than of far-reaching conclusions. The evidence is, I believe, overwhelming that the Hippoboscidae are essentially tropical insects. In spite of the well-sheltered habitat in pelt or plumage, few of them venture north and south of the Tropics and then mostly by accident. Very few have been able to gain a permanent foothold in temperate climes. Only one (*Ornithomyia fringillina*) succeeds in living during the summer under subarctic or arctic conditions. Out of a total of some 117 to 120 species from wild hosts, 92 occur in the intertropical area, 16 being mammal-flies and 76 bird-flies. On the other hand, only 52 or 53 species have been found north of the Tropic of Cancer or south of the Tropic of Capricorn, 14 being mammal-flies and 39 bird-flies. Moreover, the extratropical flies are a disparate group (Part I, p. 234): several are accidental stragglers from the tropics, known from half a dozen or fewer records in temperate regions, so that strictly speaking they are not part of the fauna; some 20 are typical tropical flies which normally extend their ranges to temperate areas, particularly the subtropical parts; the strictly extratropical flies, namely the 25 species mentioned in sections 2 to 6 above (12 mammal-flies and 13 bird-flies), are the minority. Needless to say, some border-cases must be placed arbitrarily, but they do not detract from the general validity of the grouping. The predilection of the flies for warm climates is further shown by the steady decrease in the number of species from north to south within the Holarctic Realm, as was brought out in Part I (pp. 235-236). I also pointed out that the normal northern limit for the family lies at about the 50th parallel in the New World and somewhat farther north in the Old World, and that it generally follows the annual isotherm of 30° F. (Part I, pp. 121-122). The sporadic summer records of *Ornithomyia fringillina* from north of the Arctic Circle are very few.

The detailed analysis of the specific distribution also brings out the individuality of the hippoboscoid faunae of the Eastern and Western Hemispheres. Out of a total of 122 to 125 recognizable species, 76 to 90, including 5 known only from domestic hosts, are

native in the Old World (30 or 31 on mammals and 58 or 59 on birds), and 43 in the New World (4 on mammals and 39 on birds). Of these only 8 bird-flies are common to both areas, 7 being cosmopolitan and 1 Holarctic; but, although only a small fraction of the total, these widespread species show that natural exchanges of parasitic flies occur from time to time between the two continental areas by means of the more mobile avian hosts. The Holarctic *Ornithomyia fringillina* presumably reached North America from northern Asia in post-Glacial times; but the other, more cosmopolitan flies teach us nothing about the possible routes of dispersal of the Hippoboscidae during Recent or earlier geologic periods. They could easily have attained their present distribution by natural means with the present-day topography of the continents. The scarcity of mammal-flies in the New World may be explained by the relative poverty in genera and species of Recent Artiodactyla, which are the most favored hosts of the living mammal-flies (Part I, p. 286).

It must not be overlooked that the spatial distribution of animals is by no means static, as it deals with successive populations which are in a constant state of flux. This dynamism is particularly important for the Hippoboscidae and similar parasites, where fluctuating populations of parasites depend upon populations of hosts undergoing their own fluctuations. Some of the changes involved are secular or of long range and concern more the past history of the animals; although the expansion or contraction of the area covered by the breeding hosts or their relative abundance from year to year may affect even the present-day distribution of the flies. Some other aspects of the problem were presented in Part I (pp. 224-234).

In discussing the possibility of new breeding hosts being acquired (Part I, pp. 244-246), I noted the need for observations in connection with the natural spread of certain birds to new territory. Thus far the best evidence we have in the matter has to do with the importation of new hosts by Man, several examples of which I have listed. An additional case of this type has developed recently in Scotland. Following the importation of a herd of reindeer, *Rangifer tarandus*, from Norway, it was discovered that within a few weeks after their arrival (September, 1953), the animals had become heavily infested with *Lipoptena cervi*, the common native ked of Scotch deer. The case is of particular interest because keds have never been found on reindeer in its natural

arctic and subarctic habitat in northern Eurasia, nor on its North American representative, the caribou, *Rangifer tarandus caribou*.⁹

Another aspect of dynamic distribution involves the seasonal fluctuations of the flies, treated at some length in Part I (pp. 234-244). It was assumed there that these are probably of little significance in the Tropical Zone. Data were presented, however, suggesting that in the Temperate Zone the seasonal migrations of many birds may be one of the paramount factors regulating the breeding and hence the strength and variations of louse-fly populations. Unfortunately observations bearing on this topic are so few and so fragmentary that it would be premature to draw conclusions. The problem appears to be extremely complex and will be best approached by careful studies of individual species over a large territory and in relation to all their effective breeding hosts.

EVOLUTION

It was shown in Part I that nearly all peculiarities of structure and bionomics of the Hippoboscidae are modifications of homologous or analogous features found in some of the free-living higher Diptera and that they are clearly adaptive to an almost unique type of integral ectoparasitism. The appearance and further refinement of these adaptations can only be explained logically as due to the action of Natural Selection upon genetic, hereditary variations in the process of Evolution. Taxonomy is the comparative study of the hereditary differences in morphology, physiology and behavior between the species (or groups of populations with the same inheritance) and between the higher categories of species with common characteristics. As such, it is inseparable from the study of Evolution and actually provides the only factual clues as to the lines of descent above the species level.

The following critical appraisal of the peculiarities of the Hippoboscidae, thought to be of significance in major phyletic evolution, is kept as factual as possible and stresses the present limitations of our knowledge. Conflicting theoretical views are presented in sufficient detail to enable the reader to make his own choice. In discussions of evolution a certain amount of speculation is unavoidable and can do no real harm if it is clearly distinguished from observable fact. Its chief usefulness, however, should be as an in-

⁹ I am indebted to Dr. D. S. Kettle for calling my attention to this occurrence, as well as for sending me some of the keds taken from reindeer in Scotland.

centive to renewed study of the morphology and natural history of the organisms.

For the convenience of discussion the term Proto-Hippoboscidae has been coined for the hypothetical group comprising the immediate ancestors of the Recent Hippoboscidae.

I. FOSSIL RECORD

Organic evolution being essentially a historic phenomenon, the most trustworthy foundations for a true phylogeny of Recent organisms are historical data furnished by the fossil remains of extinct forms. Unfortunately, for most higher insects and particularly for the Diptera, the fossil record is woefully inadequate. The Hippoboscidae are no exception. No fossil louse-fly was known until Statz (1940, p. 154; 1941, pp. 12-13 of reprint) described *Lynchia rottensis* (as *Ornithoponus rottensis*) from a fairly well-preserved specimen discovered in the Upper Oligocene shales (Aquitanian) of Rott (Siebengebirge, Rhineland, Germany). His description is as follows (translated from the German): "This well-preserved louse-fly is present in both the obverse and the reverse. It lies on the venter. The wings are spread out backward; the legs are in the normal position on both sides of the body. Length of body, 4.2 mm.; of wing, 4 mm.; greatest width of wing, 1.4 mm. Head rounded, as wide as long, brown, with a few setae. Eyes small, round, blackish. No ocelli. Thorax large, roundish, blackish-brown, sparsely hairy and with several long setae. Prothorax emarginate anteriorly, the humeral callosities somewhat prominent. Transverse suture of mesonotum distinct, rather stretched. Scutellum wide and short, rounded posteriorly. Wings well developed, extending far beyond the abdomen, narrowly rounded anteriorly. Surface of wing with microtrichia; veins dark brown. Costa straight, finely setose and apparently reaching $r4+5$ [apex of 3rd longitudinal]; subcosta long, parallel to costa, in which it ends. Radial veins all very strong: $r1$ [1st longitudinal] short, reaching costa before mid-length of wings; $r2+3$ [2nd longitudinal] straight, ending beyond mid-length; $r4+5$ [3rd longitudinal] stretched, ending in the anterior margin far from wing tip. All other veins very weak; $m1+2$ [4th longitudinal] slightly bent down beyond cross-vein $r-m$ [anterior cross-vein] toward hind margin, which it does not reach. Cubital vein [5th longitudinal] evenly and slightly curved, likewise not reaching hind margin. No cubital [anal] cell. Legs sparsely setose, pale brown; tarsi somewhat darker. Femora a little thickened, with strong, dark setae. Tar-

sal segments short, the last one thick, with strong, bispinose claws. Abdomen blackish-brown, about as long as, but narrower than, thorax, pointed posteriorly. Pilosity not dense; scattered long setae posteriorly. Number of segments not clear, apparently 5 or 6 before genital opening." This account and the figures (1940, Pl. 22, fig. 50, drawing of wing; Pl. 27, fig. 93, photograph of fossil; 1941, pp. 12-13 of reprint, figs. 16-17, photographs of reverse and obverse of fossil) refer clearly to a *Lynchia* (= *Ornithoponus*) similar to some of the small Recent species, so that there is no reason to doubt that it was a bird-fly.¹⁰ The preserved characters do not allow a detailed comparison with the Recent species, of which there are some 30 on a variety of hosts. Some are partial to birds of prey, others to gallinaceous game birds, waders, bustards, or rails; but only one is strictly specific of waders. It is impossible to guess the type of bird on which *L. rottensis* lived. As the species of *Lynchia* (= *Ornithoponus*) are by no means restricted to wading birds, Statz's (1940, p. 168) surmise that swamps with wading birds possibly existed at Rott during the Oligocene is not substantiated by this fossil.

Lynchia rottensis proves that the Hippoboscidae had reached their present-day maturity by mid-Tertiary and produced by then at least one of the more specialized genera of the subfamily Ornithomyiinae. The prominent humeral callosities and bifid claws of *L. rottensis* are characteristic for this subfamily while the lack of ocelli and of a closed anal cell are further specializations of certain of its members, such as *Lynchia*. It may be surmised that by mid-Tertiary probably all Recent subfamilies and genera of Hippoboscidae (and perhaps some additional ones, now extinct) were developed in their present form. This would fit in with the wealth of suitable avian and mammalian hosts known to have existed at that time. The family being by then fully mature, it must be of much greater antiquity, a conclusion which agrees with what is known in general of fossil Diptera. The order was most flourishing throughout the Tertiary, comprising up to 27 per cent of the fossil insect species known from that period, while it dropped later to about 10 per cent in the Recent insect fauna (Carpenter,

¹⁰ In Statz's paper of 1941, fig. 16 (p. 12) shows the reverse and Fig. 17 (p. 13) the obverse of the fossil (not the dorsal and ventral sides, as the captions state). Actually in fig. 17 the scutellum and the mesonotum, with the median notal and transverse mesonotal sutures, of the dorsum are very clear.

1930, p. 27). In the earlier Tertiary, particularly during the protracted Eocene, most modern families of Diptera appear to have existed, including some of the Recent Cyclorrhapha Aschiza (Syrphidae and Clythiidae [or Platypezidae]), Conopidae, and Cyclorrhapha Schizophora (Sciomyzidae). Few Eocene fossils are at present referable with certainty to the higher Cyclorrhapha or muscoids (Townsend's Oestromuscaria), from which type the Proto-Hippoboscidae were more probably derived. But, as the muscoids are represented in Oligocene and Miocene deposits by some very specialized types (such as the Glossinidae), evidently they appeared before the Eocene and probably toward the close of the Mesozoic era. In all probability primitive higher muscoid flies, of types that might have given rise to both the ancestral Proto-Hippoboscidae and Proto-Glossinidae, were already fairly abundant during Cretaceous times, if not earlier.¹¹

II. RELATIONSHIP WITH OTHER RECENT DIPTERA

The fossil record being wholly inadequate for the purpose, attempts at tracing the ancestry of the Hippoboscidae will have to rely on the comparative morphology, ecology and behavior of the Recent forms. They will have to lean heavily on structural homologies, which are sometimes in dispute. Moreover, in most holometabolous orders of Insects and especially in Diptera, it is often difficult to decide which of several peculiarities shared by two groups are due either to convergence, having been acquired independently, or to true phylogenetic kinship, being then part of a

¹¹ The evidence for the existence of higher muscoids during the Upper Eocene consists of an adult tachinid-like fly (*Lithexorista*) from the Green River formation of Wyoming and accumulations of muscoid maggots in the White River formation of Colorado. Townsend (1942, **12**, pp. 11-19) referred these maggots to 2 Recent and 2 extinct genera, claiming that 3 of the genera were true bot-flies. More probably most, if not all, of the maggots were saprophagous on dead vertebrate bodies. This agrees better with the presumed ecology of the ancient "Lake Uinta," where the White River sediments accumulated (W. H. Bradley, 1936, *Scientific Monthly*, **43**, pp. 421-430). Townsend dated the Green River deposits as Eocene and those of the White River as older (Paleocene); but American geologists now nearly agree that both formations are Upper Eocene, the White River deposits being only slightly older than the others.

common early heritage. Fortunately these difficulties are not as insuperable in the Hippoboscidae as in some other dipterous families, due perhaps to the maturity and fundamental uniformity of the louse-flies. As I attempted to do in Part I, reliable homologies can be traced for most structures, at least in the less specialized forms. The generalized features retained by the louse-flies, and which they now share with some other flies, can usually be recognized and regarded with reasonable confidence as inherited from the same or a closely allied ancestral stock.

Pupipara an Artificial Group. Latreille made the first rational attempt to subdivide the order Diptera. Like most of his contemporaries, he was so forcibly impressed by the unusual combination of integral viviparity (pupiparity), flattened, leathery body, spread-out legs and other peculiarities, that he separated the Hippoboscidae from all other Diptera, at first as a distinct order Coleostoma (1802). Although he soon returned them to their rightful place, he kept them as one of the major dipterous divisions, which he successively called Coriaceae (1803 and 1805), Eproboscidea (1809) and Pupipara (1817), as mentioned before. On the strength of Latreille's authority the term Pupipara soon came into general use for one of the two or sometimes three suborders of Diptera, to cover the Hippoboscidae, Nycteribiidae, Streblidae, and later also Braulidae. It persisted as such long after it had been shown to be untenable.

Brauer (1863, pp. 32-34) proposed the next important departure in the classification of the Diptera. He divided the order into two major groups, the Orthorrhapha and the Cyclorrhapha, on the basis of the mode of emergence of the adult from the pupa, often correlated with the presence or absence of a ptilinal suture in the head.¹² The Cyclorrhapha, as he elaborated them a few years later (1869, pp. 850-852), comprised two main subgroups: (A) Proboscidea, with the two tribes, Pseudoneura (Syrphidae) and Eumyidae (Muscoidea, Conopidae, Pipunculidae, and Platypezidae); and (B) Eproboscidea, with one tribe, Pupipara (Hippoboscidae and Nycteribiidae). This arrangement embodied some of

¹² Brauer used originally the spelling Orthorapha and Cyclorapha. This seems to have been corrected first by Schiner (1864, p. 201) to Orthorrhapha and Cyclorrhapha, the form accepted by Brauer in 1869 (pp. 846 and 850). Becher (1882, p. 53) seems to have introduced the form Orthorrhapha and Cyclorrhapha, now in common use.

the features of Schiner's system (1864*b*, p. 211), which reverted to the use of Latreille's Eproboscidea, but omitted Pupipara.

Brauer was particularly concerned with establishing that the so-called "Pupipara" of Latreille and his successors, namely the ectoparasitic pupiparous flies, could not be ranked as one of the main divisions or suborders of the Diptera, nor as a taxonomic unit distinct from and equivalent to the Myioidaria. In 1883 (p. 11) he adopted the division of his Cyclorrhapha proposed by Becher (1882, pp. 49-54) into Aschiza and Schizophora, the latter alone being provided with a true ptilinum and a ptilinal suture. Shortly afterward (1885, pp. 392-413), he discussed the matter at length in the first attempt at placing the "Pupipara" in their proper phylogenetic setting. His views were stated concisely as follows (p. 393): "The Pupipara are adaptive forms which, to judge by their entire organization may be derived from Muscoidea Cyclorrhapha, the differences they show from these being explained by and produced through their parasitic habits, so that these insects have not been ancestral to any other dipterous family, but are a terminal side-branch of the Muscoidea." It is therefore erroneous to separate them as a taxonomic unit on a par with the Aschiza and the Schizophora, or to recognize three dipterous suborders, Nemato-cera, Brachycera and Pupipara. In either of these arrangements the true relationships of the "Pupipara" are lost. Brauer stressed that, although all larval instars of the so-called "Pupipara" develop within the mother's uterus, the larva is nevertheless a typical muscoid maggot, which changes by hardening of the integument into a typical muscoid puparium. Both larva and puparium possess the characteristic seams along which the puparium of the Cyclorrhapha opens when the adult emerges. Furthermore, a specialized ptilinum is present in the adult of the so-called "Pupipara" as well as of the Schizophora. Both features could not possibly have been acquired independently, in exactly the same form, twice in the course of evolution. At the time Brauer wrote, it was not known that the free-living Glossinidae (tsetse-flies) reproduce in exactly the same manner as the so-called "Pupipara," and that the structure of the genital tract and the larva are essentially the same in both these groups. Since it is agreed that the Glossinidae are specialized Schizophora, the peculiar adenotrophic viviparity (pupiparity) of the ectoparasitic Diptera can no longer be used as a valid argument to maintain the latter as a distinct, major taxonomic unit. Brauer's conclusion that the so-called "Pupipara" are merely highly specialized schizophorous muscoids has been accepted by nearly all modern dipterists.

Brauer evidently thought that the ectoparasitic pupiparous Diptera formed one phylogenetic branch of the Schizophora, as appears from his table of the relationships of the Diptera (1883, p. 12). Here he subordinates the tribe Pupipara to the Section Schizophora, placing it on a par with the tribe Eumyidae, the latter including both the Holometopa and the Schizometopa. This arrangement now appears artificial in that it probably does not reflect the true phylogeny of these insects. As shown by the following review, there is as yet no full agreement as to whether the Hippoboscidae, Streblidae and Nycteribiidae form a monophyletic (hence natural) or a polyphyletic (hence artificial) assemblage. Their possible relationships with particular types of Recent Cyclorrhapha Schizophora and specifically with certain other Muscoidea are even more controversial.

Much of the disagreement on these two points seems to have arisen from the persistent attempts to divide the Muscoidea dichotomously in two branches, each presumably forming a distinct monophyletic unit. The two main divisions are called variously Acalyptrata (or Acalypterae) and Calyptrata (or Calypterae), terms borrowed from Robineau-Desvoidy and Macquart (Schiner, 1864, pp. 49 and 73); Holometopa and Schizometopa (Brauer, 1880, p. 117); and Haplostomata (or Athecostomata) and Thecostomata (Frey, 1921, p. 208). These names reflect the type of character given preference by the several authors to define the two groups: calypteres, type of vertex in both sexes, and hyoid (or theca); although other characters have also been used occasionally. The limits assigned to the two groups vary widely, as no two authors seem to agree as to where to draw them. In general, however, the Acalyptrata (Holometopa or Haplostomata) contain most of the more primitive muscoids, none with distinct calypteres, most of them with a broad frons in both sexes, and nearly all without a hyoid. The Calyptrata (Schizometopa or Thecostomata) comprise what are undoubtedly the higher or more evolved muscoids (and some that appear more primitive, possibly due to degeneration), many of them with well-developed calypteres and the frons narrower in the male than in the female, and nearly all with a hyoid. Although the question is strictly speaking outside the scope of the present work, I venture to submit that it may eventually be dismissed as a false problem. There seems to be no compelling reason why the early phyletic evolution of the Muscoidea, as deduced from the Recent families, should have been necessarily dichotomous. The known fossil record is far too scant to be of much help; but the

wealth and variety of Recent types suggest that the ancestral Proto-Muscoidea were subject at various times to considerable adaptive radiation ever since the Cretaceous or Jurassic. Only some, perhaps only a few, of the lineages they produced survived to the present era. It follows that the comparative study of Recent muscoids can scarcely give enough factual data to express their early phyletic evolution in a formal, trustworthy genealogy. I suggest that endeavors to trace the relationships of the several Recent families by appraising their similarities and divergences of structure, in the adult and early instars, may be more enlightening than attempts to force them into a dichotomous scheme of doubtful phylogenetic meaning.

For our present purpose we are only concerned with the monophyly or polyphyly of the so-called "Pupipara," or the degree of relationship between the Hippoboscidae, Streblidae and Nycteribiidae, and more specifically between the Hippoboscidae and the other two families.

Brauer's monophyletic theory was accepted by Handlirsch (1924, **3**, pp. 1028-1030), who united all "Pupipara" in a single family Hippoboscidae, with 2 subfamilies, the Hippoboscinae (divided into the tribes Hippoboscini and Streblini) and the Nycteribiinae.

Townsend's views, expressed in his *Manual of Myiology*, varied from time to time, but on the whole show his preference for a monophyletic origin. At first (1935, *Op. cit.*, **2**, p. 81), he combined the Hippoboscidae and Streblidae only in a superfamily Hippoboscoidea, the sole component of his subsection Nymphipara [= Pupipara] of the Diptera Schizophora, the subsection being more or less on a par with his subsection Myiodaria. At the same time he referred the Nycteribiidae to his Hypocera (Cyclorrhapha without ptilinum = Aschiza of Becher). Later (1935, **2**, p. 292; 1938, **6**, pp. 243-244; 1938, **7**, p. 429), he transferred the Nycteribiidae to his Hippoboscoidea and added to them also the Braulidae. His Nymphipara and Hippoboscoidea were defined as follows: "Head of fly more or less closely united with thorax, not freely movable; neck vestigial or much reduced." It is scarcely necessary to point out that this definition is based on trivial characters, of secondary importance in the evolution of the group, and, moreover, does not cover some of the Hippoboscidae and Streblidae, nor any of the Nycteribiidae.

Crampton (1944a, p. 154) also united the Hippoboscidae, Streblidae, Nycteribiidae, and even the Braulidae in one superfamily Hippoboscoidea. This he included among the Platypezomorpha,

the second of his two main divisions of the Cyclorrhapha Acalyptrata, defined as follows: "characterized by having a normal, well-developed sixth sternite, which (when present) is not displaced into the insect's left flank." The second section of this division, the Lauxaniiformes, he also defined: "With reduced sixth sternite. Seventh sternite not distinct, amalgamated with inverted eighth sternite, which may become atrophied." The Lauxaniiformes he divided into two superfamilies, neither of which he defined, however: (1) Lauxanioidea ("derived from the Platypezidae") containing Lauxaniidae [= Sapromyzidae], Chamaemyiidae [= Ochthiphilidae] and Diopsidae; (2) Hippoboscoidea ("derived from Lauxaniidae [= Sapromyzidae] or Platypezidae [= Clythiidae")), containing the four families mentioned above. It is difficult to see how the Hippoboscidae can have any real kinship with either the Sapromyzidae or the Clythiidae, or with the ancestors of these two families. The structure of the mouth-parts alone would seem to offer an unsurpassable objection to Crampton's view. He seems to have attached undue phylogenetic importance to supposed homologies of the male terminalia and associated abdominal sclerites. These highly adaptive structures are simplified in the Hippoboscidae, Streblidae and Nycteribiidae by loss or atrophy of many of the primitive parts, to such an extent as to be practically worthless for tracing true kinship. To decide whether the few ventral sclerites retained by some of the Hippoboscidae are modified 6th or 7th sternites would seem to be mere guesswork.

G. H. Hardy (1944) grouped all ectoparasitic so-called Pupipara in one of his nine superfamilies, the Hippoboscoidea, evidently without previous knowledge of Crampton's similar action.¹³ This superfamily he defines as follows: "Abnormal flies with coxae spaced widely apart and usually most or all abdominal segments are fused together. Parts of male terminalia are vestigial or eliminated. Flies parasitic on vertebrates." The broad, flattened sternum is the one structural character shared by all Hippoboscidae, Nycteribiidae and Streblidae, though it is not equally developed in all of them. It is due to the secondary spreading apart of the coxae, as Hennig (1941) has shown, and seems to have originated independently in several unrelated ancestral stocks of Diptera,

¹³ Hardy was not particularly concerned with the phylogeny of the several members of his Hippoboscoidea, since he stated (p. 80) that "it is convenient to retain the superfamily until the affinities can be assured."

usually though not necessarily as an adaptation to successful ectoparasitic life. At first it may have been slight in extent, in the early stages of parasitism or during the more temporary association with vertebrate hosts which presumably preceded obligate parasitism. After the ectoparasitic relations became well established, the advantages for permanent life in feathers or hair of a flattened body with laterally inserted legs increased and the sternum became gradually wider. The present similarity between the sterna of the three families is most probably due to adaptive convergence. The dorsal fusion of the abdominal segments is not a general character of the three families, being scarcely developed in the males of the Nycteribiidae and not at all dorsally in the genus *Ornithoica* among the Hippoboscidae. Moreover, it is a sequel of a gradual reduction of the hardened areas or sclerites, and this reduction varies greatly among the several genera of Hippoboscidae. Various stages of reduction of the abdominal sclerites with concomitant fusion of the softer areas occur also in other free-living, so-called physogastric Diptera, as well as ventrally in the Glossinidae, in response to the need for a more expansible abdomen in order to store food or for reproductive purposes.

Some other dipterists have offered useful suggestions regarding the evolution of the Pupipara, without committing themselves for or against the monophyletic origin of these insects. Williston (1908, p. 62) merely wrote that "*Nycteribia* and *Melophagus* are perhaps the most specialized of all insects, that is they have traveled further from the starting point."¹⁴ His acquaintance with the Pupipara seems to have been rather casual, to judge from his statement (1908, p. 58) that "it is even doubtful yet whether some of them may not be oviparous in habit; we know of one species, at least, wingless and parasitic upon birds which stands on the border line." This could only have referred to *Carnus*, which, however, has nothing in common with any of the "Pupipara." He also noted: "I believe there is a much closer relationship between

¹⁴ The oviparous Braulidae, possibly ectoparasites but more probably commensals of honey-bees, appear to be structurally much more evolved than any of the louse-flies of vertebrates. Except that they are Schizophora, they have no close connection with the "Pupipara" and should not be considered in the present discussion. They have been regarded variously as related to *Thaumatoxena*, to the Sphaeroceridae (Hennig, (1941b, p. 231), or to the Drosophilidae (Hennig, 1952, p. 325).

the Streblidae and Borboridae, than between the Borboridae and Empididae, for instance." There may be some truth in a possible collateral kinship between the Streblidae and the Borboridae; but the comparison with the relationship between the Borboridae and the Empididae is rather pointless, since the former are Cyclorrhapha and the latter Orthorrhapha.

Massonnat (1909) made an elaborate comparative study of the structural specializations of several Palearctic Hippoboscidae and one species of Nycteribiidae, including also *Braula*. Unfortunately he covered too few hippoboscid genera and did not consider the Streblidae at all. It is not surprising therefore that, in spite of his industry, his views on the affinities of these insects are couched in very general terms. Nowhere does he state clearly whether he regards the Hippoboscidae and Nycteribiidae as one or two phylogenetic branches of the muscoid stock. So far as I can gather from his concluding remarks (pp. 339-342), he recognizes that the louse-flies are allied to the Muscoidea ("Muscides"), without defining to which particular type. As for the Nycteribiidae, he is even more vague, stating only that they evolved presumably ("vraisemblablement") from the Muscoidea also (p. 341). This does not mark any real progress beyond what Brauer had established some years earlier.

Müggenburg (1892, p. 324) suspected from a comparative study of the head, antennae and mouth-parts that the Hippoboscidae and the Nycteribiidae probably had a different origin, although he recognized that both come from Cyclorrhaphous ancestors. The Hippoboscidae he was inclined to derive from the "true Muscidae" (higher Muscoidea), but offered no suggestion as to the possible ancestor of the Nycteribiidae.

Lameere's classification of the Diptera (1906, pp. 105-140; 1938, 5, pp. 71-162) is perhaps the most ambitious attempt ever made to apply the principles of phyletic evolution to the order. He prefers to accept the two suborders Nematocera and Brachycera, a slight modification of an arrangement proposed by Osten Sacken. The Brachycera he divides into Orthorrhapha and Cyclorrhapha, the latter being further subdivided much as Brauer did in 1883. He does not consider the so-called Pupipara as a monophyletic unit on a par with the Eumyidae. Instead, he includes them among the Haplostomata (Acalyptrata or Holometopa) with the remark that "probably they were derived from Haplostomata whose larvae lived in faeces, but from different types of Haplostomata" (1938, p. 145). He suggests that the Hippobosci-

dae and the Gasterophilidae had a common ancestor, that the wing venation of the Streblidae, very different from that of the Hippoboscidae, recalls that of the Helomyzidae, and that the Nycteribiidae are presumably connected with the Borboridae.

Speiser, who was no doubt better acquainted with all three families of ectoparasitic "Pupipara" than any of his contemporaries, considered the problem of their origin and later evolution in some detail (1908, pp. 425-447). He attempted to tie it up with their present geographical distribution. Such an approach could only be successful if it were possible to correlate it with the present and past distribution and migrations of the hosts. His conclusion that each family was derived from a different branch of the large muscoid stock, is based, however, on sound morphological evidence. He states definitely that each branch acquired integral viviparity (pupiparity) independently, the final similarity in this respect being due to convergent evolution (p. 426). It is evidence of his sound judgment that he is most cautious in tracing the possible relationship of each family to a particular type of free-living muscoid. He finds it nearly impossible to even surmise the phylogeny of the Nycteribiidae, because of their extreme adaptive modifications, but recognizes that some of the unique nycteribiid specializations are foreshadowed among the Streblidae. The Streblidae he regards as a monophyletic unit in spite of their great diversity, but offers no suggestion as to their nearest free-living relatives, except for a reference to the similarity in wing venation between *Nycteribosca* and the Borboridae (p. 439). He is, however, much more positive in the case of the Hippoboscidae, pointing out (p. 446) that the genus *Glossina* (in the broad sense) "is from all appearances the closest relative of the hippoboscids among the present-day muscoids."¹⁵

Muir (1912, p. 365) considers the Pupipara as polyphyletic branches of the Muscidae, in the paper in which he established that *Ascodipteron* cannot be separated from the Streblidae. Beyond this he does not express an opinion.

Falcoz (1926, pp. 8-9) is much more explicit than any earlier author. He states that the Hippoboscidae are connected with the Muscidae, through *Glossina*, a view adopted from Speiser. The Streblidae and Nycteribiidae seem to him related respectively to

¹⁵ "Dieser Gattung [*Glossina*] stehen die Hippobosciden unter den heute lebenden Musciden allem Anschein nach am allernächsten."

the Borboridae and Helomyzidae, "since they are derived presumably from cavernicolous ancestors belonging to these families and living in guano."

Jobling (1929, p. 443) originally concluded as follows, from a study of the head capsule, antennae and mouth-parts: "The structure of the head and its appendages in the Pupipara shows that the Hippoboscidae are related to the Muscidae. As regards the relations of the Streblidae and the Nycteribiidae, it is only possible to say that they are descended from the Acalyptrata. The striking resemblance, especially as regards the proboscis, is due to the phenomenon of convergence." As late as 1949 (p. 321) he maintained that "the ancestors of the Streblidae were non-blood-sucking flies which undoubtedly had some resemblance to the present Acalyptratae." More recently (1951, pp. 212 and 244), however, he changed his earlier views, after studying the thorax and abdomen more completely, and he now agrees with Hennig (1941) that the Streblidae are related rather to the Calyptrata. Either view can be correct if the Pupipara are polyphyletic. Jobling's chief merit was to point out the essential difference in the structure of the haustellum between the Hippoboscidae and the Nycteribiidae-Streblidae. In the latter, the slender portion of the haustellum beyond the swollen, bulbous base and which enters the skin, consists only of the elongated labella; whereas in the Hippoboscidae the labella are very short and only an insignificant part of the haustellum (1929, pp. 436-438).

In a detailed discussion of the phylogeny of the Diptera, Hendel (1936, pp. 1876-1877) states definitely that the ectoparasitic so-called Pupipara (or Eproboscidea) are certainly not monophyletic. Their further relationships within the Schizophora he regards as problematical, the Nycteribiidae being possibly evolved from cavernicolous (troglophilous) Acalyptrata. He considers that the Hippoboscidae are perhaps related to the Gasterophilidae which he places among the Acalyptrata. In the taxonomic section of the same work (1936, pp. 1980-1984) the three families Hippoboscidae, Streblidae and Nycteribiidae are nevertheless grouped together as "Eproboscides (Pupipara)" within the frame of the Schizophora Acalyptrata; but as this section was edited posthumously, it cannot be regarded fairly as expressing Hendel's own views.

Hennig (1941, p. 248; 1951, p. 275; 1952, pp. 400-407) has given more thought to the problem than any of his predecessors, marshalling all important available evidence. He studied in detail the widening of the ventral areas of the meso- and metathorax

characteristic of all ectoparasitic Pupipara, which pushes the mid and hind legs to the sides of the body. It should be noted that wide "sternal areas" are not restricted to the "Pupipara," but occur also in the Braulidae, which are not pupiparous and do not live on vertebrates, and in at least one of the Tipulidae (*Gnophomyia*), which are not Cyclorrhapha. Moreover, the distance between the coxae in each of the mid and hind pairs varies somewhat among the other Diptera. Hennig was able to show that the occasional unusual widening of the "sternal areas" is not due to a reversal of the cryptosterny, which is an essential feature of the dipterous thorax. The internal structures connected with cryptosterny remain unchanged, but the mid and hind coxae shift position within the original laterosternites, producing in *Hippobosca* an internal double bottom (pierced with a median window) on the ventral side of the metathorax, connected with a fold of the ventral wall of the metathorax. The widening of the sternal areas is therefore a secondary phenomenon, which undoubtedly occurred at various times independently during the evolution of the Diptera, particularly as an adaptation to successful permanent ectoparasitic life. Hennig investigated also the male terminalia, the abdominal segments and spiracles, the second antennal segment, the prestomal teeth of the labella, and the hyoid of the tentorium. These structures, he believes, suggest that the Hippoboscidae, Nycteribiidae and Streblidae are all Calyptrata. Perhaps, as I suggested, the distinction between Calyptrata and Acalyptrata is not as fundamental as is now commonly thought. In any case, it has no direct bearing on the monophyly or polyphyly of the three families, a problem the solution of which is not particularly helped by most of the structures Hennig examined.

Moreover, I am in full agreement with Hennig's general conclusion (1951, p. 275) that the ectoparasitic so-called Pupipara "are a conglomerate evolved by polyphyly and cannot be maintained as one taxonomic unit; they comprise two phylogenetically homogeneous groups, which probably should rank as families, the Hippoboscidae on the one hand and the Nycteribiidae-Streblidae on the other, both to be placed near the Muscidae." He reiterated much the same views in his recent monumental work on the larvae of the Diptera (1952, p. 401), where he pointed out in addition that the larvae of the Hippoboscidae differ in many ways from those of the Nycteribiidae and the Streblidae, although the latter two are superficially known at present in the larval instars.

Hippoboscidae a Monophyletic Family. The Hippoboscidae are so uniform in all essential internal and external structures, as well as biological features, that even the most aberrant members, such as *Myiophthiria* and *Melophagus*, are obviously louse-flies and easily placed near their more normal relatives. All agree in the much flattened head and thorax, the leathery integument, the position of the frons in a plane with the mediovertex and vertex, the flattened antennae with the 3rd segment much reduced and imbedded in the 2nd, the sheath-like palpi enclosing a needle-like haustellum, the very short terminal labella of the labium, the dorsally placed prothoracic spiracles, the broad intercoxal sternal areas bearing the legs spread out from their side edges, and the greatly simplified male terminalia. The rostrum membrane and the basal portion of the haustellum are always retractile within the head capsule. In the few genera that have been examined for the purpose, the tentorium is provided with a hyoid and the other internal structures vary only in minor details. It is most improbable that an integrated complex of so many unusual features could have arisen more than once in the course of evolution; most if not all of these peculiarities were present at least to some extent in the hypothetical Proto-Hippoboscidae. In spite of the almost complete lack of paleontological evidence, we may postulate that all Recent hippoboscids evolved from a single ancestral proto-hippoboscid stock.

The monophyletic unity of the family is also brought out by the relatively few characters available for the definition of supra-generic groups. Owing to their more primitive condition, the Ornithoicinae possess several distinctive features, namely in the antennae, frons and abdominal segmentation; but, even so, their kinship with the Ornithomyiinae is undeniable. The Ornithomyiinae also are unique in having deeply split claws and a strongly concave anterior margin of the prescutum, both adaptive specializations. None of the other four subfamilies have a single feature not shared by one or more of the others, so that each must be defined by a combination of characters, indicating how similar they are in spite of great differences in host preferences. Few of the characters of subfamilial value seem to be adaptive to a special type of host, although the appreciation of adaptiveness will always be to some extent subjective. It is more to the point that some of these characters, though present in all members of one subfamily, are nevertheless only of generic value elsewhere in the family.

The monophyly of the Hippoboscidae would scarcely call for

discussion, were it not that Bezzi (1916, p. 157) advocated a most peculiar multiple origin for the Pupipara, in which he derived some of the hippoboscids from two distinct lineages. Like many another bizarre theory, Bezzi's hypothesis is bound to fascinate those who are only superficially acquainted with the subject. It should be noted that Bezzi considered almost exclusively the few subapterous and apterous forms. He divided these in three series, one comprising hippoboscids of mammals (*Allobosca*, *Melophagus*, *Echestypus* and *Lipoptena*), another bird-flies (*Crataerina*, *Stenep-teryx*, *Myiophthiria* and *Brachypteromyia*), and a third the Streblidae and Nycteribiidae of bats. He then went on to say (translated from the Italian): "It is fairly probable that each of these series was derived by itself from a different form of higher, middle and lower Myiodaria. The phenomenon of wing reduction should be given great importance in the elucidation of their phylogeny, as yet shrouded in mystery. *Allobosca* must be a very old form, like the Australian *Ortholfersia*, which, moreover, has retained the wings; it is not possible at present to offer a hypothesis concerning its origin. The other three genera found on mammals probably evolved from higher Myiodaria related to *Calliphora*, a group containing many cuticulous forms. The genera living on birds originated probably from nidicolous acalyptrate lower Myiodaria, perhaps Dryomyzidae, a family which contains *Neottiophilum*. It seems to me that the case of *Carnus* illustrates very well the transition from a winged nidicolous acalyptrate to an apterous ectoparasite of a bird. The Old World Streblidae are possibly derived from Acalyptrata, particularly from cavernicolous Borboridae living in guano; those of the New World perhaps from other Acalyptrata, possibly Helomyzidae. The Nycteribiidae, in which the primitive shape is even more modified and which flourish in the Old World, may have had a similar origin." In so far as they concern the Hippoboscidae, these statements are certainly misleading. From their external and internal organization the louse-flies form a compact unit, regardless of the development, reduction or loss of the wings. In the subfamily Ornithomyiinae, all of which live permanently on birds only, the relationships between the winged and the subapterous forms are very close and there is no evidence that any of them could have originated from a different line of free-living ancestors; the same is true of the Melophaginae of mammals. In tracing the conjectural ancestors of the Hippoboscidae, the emphasis should be on a study of the fully-winged

genera, which have retained more of the primitive characters than the subapterous and apterous forms.

Relationship with Glossinidae. From the foregoing critical review of the opinions and evidence bearing on the problem, one may conclude that the Hippoboscidae are phylogenetically dissociated from the Nycteribiidae and the Streblidae. Further attempts to trace their origin are confronted with a complete lack of evidence, either in the Recent or in the fossil fauna, on which a hypothetical proto-hippoboscid could be reconstructed, as even the relatively primitive Ornithoicinae are too specialized for the purpose. Nevertheless, it would seem that the Glossinidae or tsetse-flies are most closely related to the Hippoboscidae among the Recent Diptera. The Glossinidae are a small, sharply defined family of free-living, blood-sucking higher Muscoidea, sharing adenotrophic viviparity (so-called "pupiparity") with the louse-flies. The two families show so many striking similarities, that the homologies of many external structures of the Hippoboscidae can most easily be traced by assuming that they are dorso-ventrally flattened *Glossina*-like flies.

Speiser (1908c, p. 446) first recognized that the genus *Glossina* was to all appearances the nearest relative of the Hippoboscidae among the present-day muscoids. Roubaud (1909, pp. 478-487) discussed some of the similarities between the two families, but concluded that they were due to adaptive convergence and not to phylogenetic kinship. Bezzi (1911, p. 119), on the other hand, claimed that the genus *Hippobosca* was closely related to the Glossinidae. In a table annexed to his paper (1911), he even derived the subfamily Hippoboscinae from the Glossinidae (or subfamily Glossininae). Bezzi thought, however, that the other Hippoboscidae did not show the same relationship, since he claimed in a later paper (1916, p. 157) that the family as a whole had a polyphyletic origin, a view with which it is impossible to concur. Zavattari (1928) extended Bezzi's theory to all the Hippoboscidae, though more specifically to *Hippobosca*, *Pseudolynchia* (= *Lynchia maura*), *Crataerina*, and *Melophagus*. His comparisons are exhaustive and should be consulted for additional details bearing on the present argument. He concluded that there is between the Glossinidae and the Hippoboscidae "a close bond of relationship and that the tsetse-flies represent a stage connecting the non-parasitic forms of Muscidae with the Hippoboscidae, obligate parasites highly adapted to this peculiar mode of life." He did not discuss the details of their phylogeny, merely agreeing with Bezzi's earlier claim that the Hip-

poboscinae were derived from the Glossinidae. At one time (1942a, p. 39, footnote) I was reluctant to follow Bezzi and Zavattari in this matter and I attributed the evident similarities between the two families partly to the retention of archaic characters shared by all primitive Proto-Myiodaria (the ancestors of both hippoboscids and tsetse-flies) and partly to adaptive convergence. A more careful comparative study of these insects, particularly of certain more generalized bird-flies (Ornithoicinae), has now led me to reverse my previous stand to some extent.

Both the Glossinidae and the Hippoboscidae are fully mature groups, sharply set off from the other Recent Diptera, as well as from each other, by an assemblage of important external and internal features. They must therefore be regarded as relatively old, since they needed sufficient time to become so highly specialized, each in its own way. The customary, well-known difficulty of appraising the relative importance in phylogeny of the several differential characters, becomes more arduous than ever in such ancient, mature and deeply modified insects. What few primitive characters may remain are not merely obscured, but actually submerged by the extreme specializations.

That the Hippoboscidae are of some geological antiquity is shown by their highly evolved structure. It is further supported by the recent discovery of an Oligocene species of *Lynchia* (discussed before) as fully specialized as any of the Recent forms of this genus. The evidence that the tsetse-flies are at least equally ancient is even clearer. Several recognizable species of Glossinidae are known from the Florissant shales (Miocene) of North America, showing that the family was flourishing and possibly cosmopolitan during late Tertiary. The most surprising feature of these fossils is that they differ only in minor details from the Recent African species. We are forced to the conclusion that the ancestral Proto-Glossinidae must have lived during the Eocene or possibly late Cretaceous periods. If both the Hippoboscidae and Glossinidae arose from a common muscoid-like stock, this ancestral group must have been even older, possibly dating from the middle Mesozoic.

The free-living Glossinidae have retained more of the primitive muscoid features than the ectoparasitic Hippoboscidae, the several parts of the body and the appendages being shaped much as in the common muscoids, such as the house-fly (*Musca*). Like these, the tsetse-flies have the head (Part I, p. 16, Fig. 3D) vertical, swollen and hemispherical, freely movable on a narrow neck connecting the center of the occiput with the pronotum. The frons, or long an-

terior vertical area of the face, forms an angle with the vertex or posterior, nearly horizontal part. The small clypeus is a short, transverse sclerite beneath the anterior margin of the frons, at the extreme base of the proboscis. The eyes are large, broadly separated in both sexes and bare; 3 ocelli are well developed. The antennae, placed close together on a small lunula, fill most of a median, undivided, deep antennal cavity (depressed frons) below the ptilinal suture and between the strong lateral facial ridges. The 1st and 2nd antennal segments are very small, the 2nd split on the outer surface over its whole length; the 3rd is very long and bears near the base a thick, twice-feathered arista, with a single outer row of long, soft setae, each in turn provided with 2 rows of short hairs. The proboscis, hidden at rest between the long, straight, cylindrical maxillary palpi, forms a straight, needle-like haustellum whose structure duplicates that of the Hippoboscidae, but which is not retractile at the base. The thorax (Part I, Figs. 8B, 9B, and 10B) is slightly depressed, though scarcely more than in some other Muscoidea. It shows the usual sutures, furrows and dividing lines, as well as most of the groups of bristles, of the Calyptrata; the hypopleurite (meropleurite 2) lacks hypopleural bristles. Malloch (1929, p. 553) noted the absence of the sclerotized "prosternal plate" (Ferris' intercoxal area of preëpisternum) found in other Calyptrata and correlated this with the bulbous base of the haustellum. The subscutellum, behind and below the scutellum, is distinct but moderately convex. The prothoracic spiracles are on the vertical sides of the propleura, rather far down. The legs are long and inserted beneath the thorax in the usual muscoid manner, close to the median sternal line. The coxae in each pair are narrowly separated by a slight secondary widening of the sternal area. The claws are long, slender, curved, simple, without strongly developed heel; the two pulvilli are very broad, pad-like, with many minute tenent hairs on the under surface; between the pulvilli there is a bristle-like empodium. The wings are well-developed and show a typical muscoid venation with four complete cross-veins in the disk (anterior cross-vein or *r-m*; discoidal cross-vein or *m*; anterior basal cross-vein or *M*₃; and anal cross-vein or *Cu*₂); the apical stretch of the 4th longitudinal vein is straight, not bent nor angular. A characteristic feature of the venation is the strong downward bulge of the first basal cell at the anterior cross-vein, also present, moreover, though less marked, in one of the Hippoboscidae (*Olfersia sordida*). The membrane of the wing is finely and somewhat radiately rilled, and entirely cov-

ered with very small microtrichia (also over the alula and both calypteres). The two calypteres or squamae, as well as the alula, are well developed, the calypteres differing only moderately in size. The halteres are large, not hidden by the calypteres. The dorsum of the abdomen is completely covered by clearly divided, sclerotized tergites, which, however, stop sharply at the lateral edges. The ventral integument is soft, membranous; except for a fairly large sclerotized basal sternite, followed by a minute median sclerite, its segmentation is merely indicated by transverse folds. The 7 pairs of spiracles lie in the ventral membrane close to the edges of the tergites. The male terminalia are large and elaborate; at rest they are folded beneath the tip of the abdomen and completely hidden by a reflexed dorsal sclerite. The internal anatomy is similar to that of the Hippoboscidae, particularly in the structure of the genital organs. The single oesophageal diverticulum or storage crop is, however, functional and expands greatly when filled with blood. The integral or adenotrophic viviparity duplicates almost exactly that of the Hippoboscidae; but the newly-voided, full-grown third larval instar is sufficiently mobile to burrow in loose soil or dirt. The larva and puparium are like those of the Hippoboscidae, particularly in the presence of terminal respiratory swellings, which are even more pronounced than in the louse-flies.

At first glance, the Hippoboscidae differ greatly from the tsetse-flies, owing to the strong dorso-ventral flattening of the body, particularly of head and thorax. This has entailed shifts in the relative position of certain areas, fusion of some of the sclerites, and especially a considerable extension of the sternal areas between the insertions of the coxae. If these features are taken into account, there is little difficulty in correlating the various areas of the head and thorax of a hippoboscid with those of a tsetse-fly. One major discrepancy is in the structure of the hippoboscid antenna, which by no feat of the imagination can be derived from that of *Glossina* and is an important evolutionary departure from the hypothetical common ancestral muscoid stock. On the other hand, there is little difference in the proboscis, except that in the louse-flies the bulbous base and much of the needle-like portion of the haustellum are retractile within a ventral pouch formed by the rostrum membrane, when not in use. The similarity of the mouth-parts, even in detail, between the two families is astounding, considering the many and far-reaching changes involved in developing such a specialized proboscis from the usual, primitive "sponging"

type of most Muscoidea. Likewise, the structure of the internal genital organs of both sexes is almost the same in the Glossinidae and Hippoboscidae, as is also the type of adenotrophic viviparity. There is, however, much difference between the two families in the structure of the external male terminalia. The wing venation varies within the family Hippoboscidae and does not indicate true relationships. While that of *Hippobosca* differs conspicuously from the tsetse-flies, that of the more primitive *Ornithoica* is more like them, differing essentially only in the lack of the discoidal cross-vein. The absence of the discoidal cross-vein, resulting in the fusion of the discal and 2nd posterior cells, is an outstanding peculiarity of all Hippoboscidae. The rilled wing membrane of Glossinidae is present also in *Hippobosca*, but absent or barely indicated in other louse-flies. The development of the alula and calypteres varies greatly in the Hippoboscidae.

While it seems impossible to derive the Hippoboscidae directly from a tsetse-like ancestor, it is most improbable that the complex specializations of the mouth-parts and of the inner reproductive organs could have arisen independently on two occasions from ancestral muscoids and then developed further to the point of almost exact duplication. A more logical surmise is that the free-living Glossinidae and the ectoparasitic Hippoboscidae are diverging, ancient offshoots from a single stock which had previously acquired both the same type of sucking haustellum and integral, adenotrophic viviparity. As the body structure of tsetse-flies does not suggest an earlier adaptation to permanent ectoparasitism and it is unlikely that a permanent ectoparasite would return to a free blood-sucking life, the common ancestors may safely be stated to have been free-living. At the same time they were most probably mainly, if not wholly, hematophagous, as suggested by the fact that in the Recent fauna all known insects with integral viviparity are restricted to a diet of vertebrate blood. The kinship between the Hippoboscidae and the Glossinidae is therefore collateral and based only on a very ancient common ancestry.

III. EARLIEST HOSTS OF HIPPOBOSCIDAE

The origin and further differentiation of the louse-flies are obviously tied up with the rise and evolution of the vertebrate hosts, so that it would be helpful if the original type of host could be determined with some degree of probability. In the absence of positive clues based on the fossil record, one can only speculate. The view expressed some years ago (J. Bequaert, 1942a, p. 41) that the

true Hippoboscidae or their ancestors, the Proto-Hippoboscidae, became established permanently first on birds, still appears most probable. If such was the case, the mammal-flies were derived later and at various times from several bird-flies, all of which had previously acquired the essential family characteristics.

The present-day Hippoboscidae are restricted to warm-blooded vertebrates and there is no reason to suppose that the ancestral Proto-Hippoboscidae evolved on anything but homoiotherm hosts. Hennig (1941b, p. 247) mentions Speiser's suggestion that the ancestors of the Hippoboscidae might have been parasites of reptilian ancestors of birds and mammals and rightly dismisses the idea as fantastic.¹⁶ The problem of the original hosts is thus restricted to a choice between birds and mammals.

1. In the Recent fauna bird-flies far outnumber those of mammals in genera and species. Of the 20 genera here recognized as valid, with 121 to 124 recognizable species, 12 genera (60 per cent) with 88 to 90 species (72 per cent) live normally on birds only and never breed on another type of host. Nevertheless, these bird-flies form only two lines of descent or subfamilies: the primitive Ornithoicinae (1 genus with 6 or 7 species) and the more advanced Ornithomyiinae (11 genera with 82 or 83 species). One additional bird-fly belongs in the Hippoboscinae. On the other hand, the far fewer louse-flies of mammals, 33 or 34 species in 8 genera, are placed in four subfamilies: the Hippoboscinae (1 genus with 7 species on mammals), the Alloboscinae (1 genus with 1 species), the Ortholfersinae (2 genera with 4 or 5 species), and the Melophaginae (4 genera with 22 species).¹⁷ Of course, the argument based

¹⁶ It seems doubtful that Speiser (1908c, p. 446) was as definite in his statement as Hennig implies. The passage to which Hennig seemingly alludes is so nebulous that I do not venture to translate it, but prefer to cite it in the original German: "*Glossina* saugt nach R. Koch mit Vorliebe das Blut der heutigen grossen Saurier, der Krokodile, *Ortholfersia*, nahezu die ursprünglichste unter den Hippoboscideengattungen, bewohnt Beuteltiere! Einmal von Sauriern über Beuteltiere zu höheren Säugern, und zweitens von einer *Glossina* ähnlichen Fliege über *Ortholfersia* ähnliche Tiere zu den heutigen Hippobosciden?" I may point out that *Ortholfersia* is a highly specialized fly as compared with the much more primitive *Ornithoica* of birds.

¹⁷ Future discoveries will alter the absolute numbers of recognizable species and perhaps even of genera; but they will probably not affect appreciably the ratio of bird-flies to mammal-flies.

on the present-day relative strength is open to objections. First, not all the smaller subfamilies are restricted to mammals. Furthermore, these small subfamilies are probably all relicts of relatively archaic groups, of which only a few species survived in the Recent fauna, so that it might be important to know their approximate geologic age, concerning which the fossil record is silent. It is true that the only known fossil hippoboscoid (*Lynchia rottensis*) is unquestionably a bird-fly; but it is so similar to the living species and is of such relatively late age (Oligocene), that it throws no light on the problem. The very fact that the Recent Ornithomyiinae of birds are more prolific and, in addition, show signs of relatively late evolution, as shown in the sequel, might conceivably point to a more recent origin for this subfamily. It could indeed be argued that louse-flies became more numerous and more varied on birds merely because the soft and dense plumage offered them a more favorable environment than the coarser and looser pelt of mammals, on which the ancestral Proto-Hippoboscidae (in this view) possibly had originally acquired the ectoparasitic habit.

2. All Recent Hippoboscidae are highly modified from the original muscoid type and, as the fossil record shows, they were so by mid-Tertiary at the latest and presumably much earlier. It is therefore difficult to recognize and appraise the primitive characters retained by the several subfamilies. Specialized types occur both on birds (*Myiophthiria*) and on mammals (*Melophagus*). *Melophagus* is often regarded as the extreme specialization among the Hippoboscidae; but I shall attempt to show later that *Myiophthiria* is better entitled to this distinction. It is true, nevertheless, that the most generalized louse-flies known (Ornithoicinae) are found nowadays on birds only. Moreover, some of the fully-winged Ornithomyiinae are decidedly more primitive than any of the winged louse-flies of mammals. This type of argument may be somewhat more convincing than the first; although it could be objected that the extreme specialization of some of the Recent mammal-flies predicates a very long evolution on the same general type of host, possibly older than that of the bird-flies.

3. The early geologic history of birds and mammals may conceivably throw further light on the problem. As shown before, the hypothetical Proto-Hippoboscidae originated, presumably during Cretaceous times (mid to late Mesozoic) or even earlier, from a free-living, blood-sucking, pupiparous myiodarid stock, by acquiring the habit of remaining permanently on the vertebrate host between blood meals. If they were induced to stay on the host,

either by the constant and higher temperature of the skin or the search for greater security in the body cover, which seems at least plausible, a dense cover of finely divided, soft, overlapping feathers may have been more attractive and more suitable than the simple, relatively loose and often coarse pelt of most mammals. Birds, as compared with mammals, offered an added advantage to the flies in that their thinner and softer skin is more easily pierced by the mouth-parts.

As is well known, both the true mammals and the true birds started independently from terrestrial reptilian stocks at about the same time in the Earth's history. Geologically speaking, mammals are slightly the older, as first traces of them appear in late Triassic deposits, while the oldest known birds date from the Jurassic (Lambrecht, 1933; Howard, 1950). However, birds seem to have become differentiated to their present variety more rapidly than mammals and consequently may have offered sooner a prolific choice of types attractive to ectoparasitic flies. The earliest Jurassic birds were perhaps only sparingly feathered, much of the body being possibly covered with scales or structures transitional between scales and feathers. During the Cretaceous, however, there were several dissimilar types of birds, some of them essentially similar to Recent forms (Lambrecht, 1933; Howard, 1950). There is little doubt that many Cretaceous birds had a plumage fully adequate for ectoparasitic insect life. Meanwhile the primitive mammals persisted; but the Mesozoic fossil record shows only a few types all of small size (averaging that of rats and mice), similar in appearance and possibly also in habits to the Recent Insectivora. What their pelt was like or whether they even had hairs instead of scales, is unknown. It may be pointed out that no Recent Hippoboscidae are known from the orders containing only small mammals, specifically from the Insectivora and Rodentia. The scarcity and small size of the Mesozoic mammals seem to make them most improbable hosts for the ancestral Proto-Hippoboscidae, particularly as many more satisfactory bird hosts were available. There is, moreover, every reason to believe that the Hippoboscidae had acquired most or all of their characteristic features of structure, physiology and behavior before the close of the Mesozoic or early in the Cenozoic.

In this connection, I have shown (Part I, pp. 246 and 313-314) that there is a sharp contrast between the large variety of types of birds used for breeding by Recent louse-flies and the few types of mammal hosts. While the bird-flies are associated with 18 out of

the 27 major groups or orders of Aves, the hosts of the mammal-flies belong to only 5 out of the 18 orders of Mammalia. Moreover, most mammal-flies live on Artiodactyla and only a few are associated with Carnivora (*Hippobosca longipennis*), Marsupialia (in Australia only), Primates (lemurs, in Madagascar only), or Perissodactyla (in domestication only).

4. In the discussion of the probable origin of the ectoparasitic habit which is to follow, I suggest that the earliest stages of the structural adaptations to ectoparasitism may have been acquired when the ancestors of the Hippoboscidae were blood-sucking muscoids living as yet freely in or near the nests of the hosts. The need for adequate shelter between meals was possibly the original selective factor determining a gradual flattening of the body and spreading of the legs. If this was the case, the nesting habits and types of nests of birds were probably more suitable for such an evolution than the burrows or other temporary resting places of most mammals. As noted before (Part I, p. 120), the adaptive structures now characteristic of the Hippoboscidae seem to be more advantageous in plumage than in pelt and are also more marked in the bird-flies.

The foregoing considerations seem to warrant the conclusion that, although no certainty can be reached in the matter, birds were most probably the first hosts of the earliest true Hippoboscidae. It follows that all mammal-flies must have been derived from bird-flies. The further discussion of the evolution of the family will be based on these two conjectures.

IV. EVOLUTION WITHIN THE FAMILY

All Hippoboscidae, from the most primitive (*Ornithoica*) to the most specialized (*Melophagus* and *Myiophthiria*), have an unmistakable family air, due not so much to the depressed thorax and spreading legs (also found in the Streblidae and the Nycteribiidae) as to the wedge-shaped head with the flattened face and large eyes (present in no other Diptera). These features and some others are clearly adaptations to obligate ectoparasitism on warm-blooded vertebrates covered with feathers or hair (Part I, p. 120). It may be of interest to inquire whether closer adaptive correlations can be recognized between the several types of louse-flies and the taxonomic kinship or ecological peculiarities of their special breeding hosts. From what is to follow it would seem that such correlations are exceptional above the generic or specific level of the flies.

The evolution of the Hippoboscidae no doubt paralleled that of

their vertebrate hosts. A wealth and diversity of appropriate hosts must have resulted in an abundance and variety of louse-flies. The evolution of birds seems to have been more gradual, less explosive and more conservative than that of mammals, and relatively more of the major groups (orders) it produced seem to have survived to the present day. By Eocene times most of the Recent orders of birds were clearly distinguishable and several family divisions were apparent (Howard, 1950, p. 4, fig. 1). These circumstances possibly explain why the Recent bird-fly fauna is at once richer in species and genera and more uniform in supra-generic characteristics. In marked contrast, the few Recent louse-flies of mammals belong to four distinct subfamilies, each of which seems to have evolved by itself from its own ancestral bird-fly. The many successive Tertiary types of mammals offered excellent opportunities for the development of such mammal-infesting flies.

There is actually no single character or set of characters separating all mammal-flies from all bird-flies, although certain peculiarities or tendencies may be more marked or more frequent in one of the groups. This statement remains true even if we choose to ignore the one species of *Hippobosca* of the ostrich as a taxonomic aberration. All louse-flies, of mammals as well as of birds, have two claws on every leg, although the claws are sometimes unequal in the pair in the mammal-flies. While the bird-infesting Ornithomyiinae have claws with split tips, and the Hippoboscinae, Melophaginae, Alloboscinae and Ortholfersiinae of mammals have simple-tipped claws, the Ornithoicinae of birds have simple claws like the mammal-flies. Split claws may be useful to the bird-flies in helping to adhere to the feathers and may thus have a decided adaptive advantage; but *Ornithoica* shows that they are not essential for survival in plumage. On the other hand, simple claws are quite suitable to life in pelt and were therefore retained by the mammal-flies from the primitive Proto-Hippoboscidae, which it is believed first developed on birds. Various other characters are sometimes claimed to be peculiar either to bird-flies or to mammal-flies, such as the shape or size of the antennae, the thick or slender shape of the legs, and the presence or absence of ocelli, but only because of superficial acquaintance with the family as a whole. Müggenburg (1892, p. 320) noted that the haustellum of the mammal-flies he examined (*Melophagus*, *Lipoptena* and *Hippobosca*) was very slender, whereas that of the bird-infesting *Crataerina* was relatively shorter and thicker. He correlated this with the thinner skin of birds, which is also more poorly provided with

capillaries than that of mammals. He thought that bird-flies required only a relatively short haustellum, but one making a wider gash than the longer and more slender haustellum needed to imbibe blood from a mammalian skin. A comparative study of the haustellum throughout the family shows, however, that the supposed difference is so slight and so difficult to appreciate, that it could not be used as a subfamily character.

The relatively few apterous and subapterous flies show more marked structural adaptations to definite types of hosts than the fully-winged forms. The two completely apterous species of *Melophagus* are eminently adapted to life in the dense under wool of their very special hosts. The subapterous *Crataerina*, *Stenep-teryx* and *Myiophthiria* also are built ideally for survival in the closely packed plumage of the fast-flying swifts and swallows, to which they are wholly restricted. As described in the sequel, the special adaptations of these flies are foreshadowed in certain fully-winged species of *Ornithomyia* likewise restricted to swallows.

No such close correlations between structure and type of host can be traced among the fully-winged louse-flies, whether of birds or of mammals. As a rule it is impossible to surmise on purely morphological grounds what type of host a fully-winged fly might prefer. The dearth of special adaptations is obviously correlated with the low degree of host-specificity of many of these flies. It is well illustrated by the genus *Lynchia*, the largest of the family, in which some species breed successfully on a variety of unrelated birds (*L. americana* on members of 3 orders), while others are more host-restricted but prefer different types of birds (*L. hirsuta* on Galliformes; *L. nigra* on Falconiformes and Strigiformes; *L. albipennis* on Ciconiiformes; *L. angustifrons* on Falconiformes; *L. pilosa* on Otididae in the Gruiformes; *L. holoptera* on Rallidae in the Gruiformes; etc.). The structural characters separating these species are scarcely adaptive to the particular type of preferred host; so that the host selectivity of these flies must be correlated with physiological or ecological adaptations. Similar conditions prevail in *Olfersia* among the bird-flies and *Hippobosca* among the mammal-flies. In addition, *Hippobosca* has evolved a species restricted to a bird, the ostrich, and this fly shows no great morphological departure from its congeners.

In the Hippoboscidae, the dearth of Recent genera and species contrasts sharply with the structural diversity as expressed by the six subfamilies. Each of these appears to be a distinct line of descent, as no connecting links are known. The distinctiveness of

the subfamilies suggests that they are ancient lineages, presumably remnants of an early, more profuse adaptive radiation of the louse-flies which reached its peak when the mammals and birds were at their height and has declined ever since. The peak may have been during the Miocene, when the Artiodactyla, now the chief hosts of the mammal-flies, were also particularly flourishing. Facts based on the fossil record are lacking to allow further speculations about the origin of the subfamilies.

It is possible, however, to recognize within some of the subfamilies certain trends of evolution, often correlated with host-specificity. They are not claimed to represent actual lines of descent, but merely illustrate some of the types of change which occurred in the course of the past evolution of the family.

1. **Ornithoicinae the Most Primitive Hippoboscids.** The Ornithoicinae are of unusual interest because they are indubitably the most primitive Recent hippoboscids. Typical Hippoboscidae in all essential characters and easily recognized as such, they nevertheless retain some features believed to have been characteristic of the hypothetical Proto-Hippoboscidae. The first antennal segment is large and completely divided from the frons; the interantennal area of the frons (frontal carina) is very narrow, sunken and not visible between the paired first antennal segments, which are in contact on the middle line; ocelli are present; the thorax is moderately flattened, with a nearly straight anterior prescutal margin and broadly rounded, barely projecting humeral callosities; the notopleuron is completely separated from the prescutum; the prosternum forms an undivided, trapezoidal sclerite between the fore coxae; the tarsal claws are simple; the wings are functional throughout adult life and provided with a large alula and the complete venation for the family; in both sexes the dorsum of the abdomen is extensively covered by large median sclerites. The only known genus is world-wide and most of the few species are polyxenous on many unrelated birds.

2. **Evolution in the Ornithomyiinae.** Sharply contrasting with the Ornithoicinae, the Ornithomyiinae contain some of the most specialized louse-flies and certainly the most evolved of the bird-flies. This is shown by the following combination of characters all of them share. The first antennal segment is very small and more or less fused with the lunula; an interantennal frontal carina separates the two antennae; the thorax is much flattened, with a deeply emarginate anterior prescutal margin and strongly projecting humeral callosities; the notopleuron is often partly or

wholly fused with the prescutum; the prosternum is deeply divided into two lobes; the tarsal claws are bifid; the median dorsal sclerites of the abdomen are reduced or lacking. Some of the species are polyxenous, but others are among the most narrowly specific flies known.

I recognized in the subfamily Ornithomyiinae 4 subgroups on the basis of closer relationship, and gave one of these tribal rank. Three of the subgroups comprise too few genera or species, differing only in minor details, to show definite evolutionary trends. In the subgroup of 5 genera including *Ornithomyia*, however, certain orthogenetic changes are clearly correlated with special hosts, host-specificity being often more pronounced than usual. The series leading from the fully-winged *Ornithomyia* to the subapterous, flightless *Myiophthiria* is one of the most instructive sequences of evolutionary stages I am acquainted with among insects (J. Bequaert, 1943a, pp. 109-112). It is best understood by following first the gradual reduction of the wings. The common, more generalized species of *Ornithomyia*, such as *O. avicularia* and *O. fringillina*, have long, fully-developed wings, with a complete venation, and are as good fliers as any other winged hippoboscid. In the Old World group of *Ornithomyia biloba*, as well as in the American subgenus *Pseudornithomyia*, there is a decided shortening of the wing, the venation remaining normal, although the veins tend to crowd toward the anterior margin. Further reduction of the wing, eventually culminating in the functionless condition, apparently proceeds along two different lines. In one, leading to *Stenepteryx*, the wing retains its full length, but has lost most of the posterior membrane, while some of the veins disappear and the remainder crowd near the costa. In the other, leading through *Crataerina* to *Myiophthiria*, the whole wing is shortened with crowding or loss of most of the venation, until in *Myiophthiria* it is reduced to a short, broad flap, barely extending beyond the scutellum and with a few thickened rudiments of veins. All known species of the 3 subapterous genera are incapable of flight. Moreover, the reduction of the wings is accompanied by other changes affecting nearly all parts of the body. The most striking of these are: the lengthening of the head; the reduction of the compound eyes; the atrophy or loss of ocelli; the extreme development of the humeral callosities; the obsolescence of the dorsal thoracic sutures; the gradual disappearance of most of the tergal sclerites of the abdomen; the unusual development of the legs, particularly of the deeply cleft claws; and the increased pilosity. It is of interest that

these changes progressed farther in some species than in others. The American *Crataerina seguyi* is clearly less evolved than its Old World congener, *C. pallida*, and hence easier to recognize as a modified *Ornithomyia* of the *biloba* type. On the other hand, as pointed out before (J. Bequaert, 1943a, p. 109), the Old World species of *Myiophthiria* are slightly more specialized than the American, so that there is some reason to retain the subgenus *Brachypteromyia* for the New World forms.

The choice of a restricted and peculiar type of host was, it seems, the main factor determining this orthogenetic evolution. The more generalized species of *Ornithomyia* of the *avicularia* group show little host-specificity, being found on a variety of passerine and game birds, even sporadically on birds of prey; but those with shortened wings of the *biloba* group use only swallows and martins (Hirundinidae) as regular breeding hosts. *Stenopteryx hirundinis* also lives normally on swallows, though straying occasionally to swifts (Apodidae). The Old World species of *Crataerina* and all species of *Myiophthiria* are restricted to swifts, at least for breeding; but the one American *Crataerina seguyi* is associated with swallows only. Evidently the ancestors of the swift-flies were swallow-flies and the shift from swallows to swifts as hosts induced the series of evolutionary changes in structure eventually culminating in *Myiophthiria*.

As in most such cases, both the original selective factor which initiated the changes and the later adaptive mechanism involved elude us as yet; but the end result may be recognized as an efficient adjustment to the special morphology and habits of the hosts. Swallows and swifts are among the most aerial of birds, with the swifts by far the speedier of the two groups. Some species of swifts are possibly the fastest birds for their size, sometimes reaching 70 to 100 miles per hour.¹⁸ Both swallows and swifts are also capable of long-sustained flight, as they catch their food on the wing; but, again, swifts spend much longer uninterrupted periods in the air, some species being unable to perch. When not nesting, they may stay aloft at one stretch for the major part of a day. In swallows and even more so in swifts, the narrow pointed wings, very long in proportion to the small body, and the frequently forked tail (with the fork capable of opening and closing) are clearly adaptations to a predominantly aerial life. The body and

¹⁸ These appear to be the most reliable estimates of the speed in flight of these birds (further details in J. Bequaert, 1943a, p. 111).

particularly the head are built so as to offer the least resistance to the air, both being perhaps more streamlined in swifts than in swallows. The plumage is very even and smooth at the surface. That of swifts is usually coarser, stiffer, with less down on the base of the body feathers, than that of swallows.¹⁹ Several of these features fit in well with structural peculiarities of their parasitic flies. The reduced or atrophied wings decrease the risk of the fly's being blown off the host travelling at high speed. Fully-developed wings are also of no further use for reaching a new host, since the bird spends so much of its life in mid-air and away from the nest. The larvae are deposited in the nests, where the adults emerge and new hosts are usually available, at least during the breeding season. The lengthened head and more than usually flattened, nearly wingless body, as well as the strong, spider-like legs, enable the fly to glide swiftly through the dense, coarse plumage, where it can take a firm hold on the feathers with the exceptionally strong legs and the long, deeply split claws. The many long, stiff setae covering the body, legs and the costa of what remains of the wing, also help the fly to stick to the feathers like a burr. The obsolescence of the thoracic sutures is a sequel to the disuse of the wings and is of doubtful direct use to the insect. This applies also to the reduction of the compound eyes and loss of ocelli, the atrophy of the organs of sight generally following the loss of the power of flight in Diptera.

Speiser (1899c, p. 122; 1908c, p. 425; 1909a, p. 102) correlated the subapterous condition of *Stenepteryx*, *Crataerina* and *Myiophthiria* with the nesting habits of the swallow and swift hosts. Most of these birds build fairly permanent nests, many of them often assembled in colonies, the birds returning to the same colony and even using the same nests year after year. Two of the genera of flies (*Stenepteryx* and *Crataerina*) are known to larviposit in the nests and *Myiophthiria* probably does likewise. In temperate regions the puparia pass the winter in the empty nests after the fall migration. Upon the birds' return in the spring, newly-emerged flies, though flightless, have little difficulty in reaching the right

¹⁹ The similar adaptive peculiarities of swifts and swallows were acquired independently, as the two groups are not related, being placed in distinct orders by modern ornithologists. It may be of some interest to us that the swifts (Apodidae) date probably from the Upper Eocene, fossil remains being known from the Oligocene to date.

host by running, either in the same or in a nearby nest. Subapterous species of bird louse-flies could scarcely survive unless the nests of their hosts were congregated, as well as fairly durable. It is also no doubt true that flies living on birds that nest in colonies no longer need wings in order to reach the host after emerging. Nevertheless, it is difficult to conceive how the host's gregarious nesting habit alone could have been a selective factor powerful enough to induce the gradual reduction of the wings, as well as the several concomitant changes in body structure mentioned above. Gregarious nesting habits of the hosts have not always been followed by their louse-flies losing the power of flight. Some of the species of *Ornithomyia* mentioned above as specific parasites of swallows have retained the wings and make full use of them. Likewise, the species of *Olfersia* associated with oceanic or marine birds, most of which nest in large colonies or permanent rookeries, are good fliers and show no tendency toward a reduction of the wings.

The evolution of *Crataerina* from an *Ornithomyia*-like bird-fly (though not from one of the Recent species) is obvious. It seems unnecessary to do much more than mention a recent suggestion (Legendre, 1952) that *Crataerina pallida* had "ancestors in the distant past parasitic of mammals" and that it "became adapted secondarily to birds." *Crataerina* could not possibly be derived from any known type of mammal-fly and it has all the essential characters of the other Ornithomyiinae of birds.²⁰

3. Evolution of Louse-flies of Mammals. Although the bird-flies of the more specialized subfamily Ornithomyiinae are at present the dominant hippoboscoid group, there is no compelling reason why this should always have been so. If the mammal-flies evolved from bird-flies, as seems most plausible, the shift from birds to mammals may have occurred on several independent occasions,

²⁰ The author's notion that the bristles of the head and scutellum of *C. pallida* are "ctenidia-like" or that those of the scutellum form a "true ctenidium" is based on a misapprehension of the nature of the ctenidia found in most Nycteribiidae and some Streblidae. The bristles of *Crataerina* are actually not stiffer, not more numerous and not more slanting than in some fully-winged bird-flies or even some free-living muscoids. Those on the scutellum of *C. pallida* are ordinary bristles, unequal in length and thickness, irregularly scattered over the surface and a long way from forming a ctenidium.

each time starting from a different type of bird-fly. Only four such lineages survived to the Recent Era, mostly as a few relicts; but it seems reasonable to surmise that other similar mammal-infesting lines of descent are now extinct. Presumably the mammal-flies flourished during the Age of Mammals, which reached its peak during the Oligocene and Miocene, rapidly declining later.

The Recent mammal-flies all have simple claws and humeral callosities either not, or only moderately, projecting along the sides of the head, two primitive characters retained also by the Ornithoicinae of birds. It would appear then that their ancestors shifted to mammalian hosts fairly early in the history of the true Hippoboscidae, when the majority of the bird-flies were less specialized than the Recent Ornithomyiinae.

A consideration possibly of some evolutionary significance is the relative size of the bird-flies and mammal-flies. In the Recent fauna, the primitive Ornithoicinae of birds are very small, in fact the smallest of the louse-flies. The more specialized Ornithomyiinae of birds are all larger and include the largest hippoboscids known (*Ornithoctona*). Some of these large flies live on relatively small birds. The gradual increase in size on birds was made possible by the excellent protection offered by the feathers against destruction by the host, always the most dangerous enemy of the flies. Recent mammal-flies are medium-sized (Hippoboscinae) to small (Melophaginae), in spite of the average larger size of their hosts as compared with the majority of birds. The small size allows for better adherence and greater safety in the rather short and loose pelt of most mammalian hosts, and may have been retained by the mammal-flies from the ancestral bird-fly stocks, making it plausible that the earliest, primitive true hippoboscids were small insects.

In addition to the two primitive characters mentioned above, all mammal-flies share one specialized feature, namely the broad and flattened interantennal area of the frons, in which the lunula and frontal carina are completely or mostly fused. This peculiarity is, however, also present in *Olfersia*, a genus of bird-flies in the subfamily Ornithomyiinae, indicating that the specialized frons was possibly acquired at a later date and independently by each of the four side-branches of mammal-flies.

The early history of the mammal-flies is entirely conjectural. It can be guessed partly by considering the specializations of the Recent forms, as was done in previous paragraphs. Additional light may perhaps be thrown on it by a brief consideration of the

evolutionary history of the Class Mammalia, which, in so far as it concerns the present problem, has three outstanding features. (1) A tremendous adaptive radiation, which for number, diversity and extent of the resulting types far exceeds that of any other comparable group of animals during a similar span of time. (2) The extraordinary rapidity with which this far-reaching diversity was produced. After a rather slow start during the latter half of the Mesozoic, the mammals differentiated tremendously during the first half of the Tertiary, so that by Oligocene and Miocene times their evolution had reached its peak. (3) The even more rapid decline of the Class at the close of the Tertiary, particularly during Pleistocene and Recent times. According to Simpson (1945, p. 35), the known mammals, both living and extinct, belong to about 3000 well-defined genera, representing 32 distinct major groups (or orders), subdivided into 257 groups of lesser importance (families). Of these, however, only about 1000 genera, representing 118 families and 18 orders, survived to the Recent era. Since the knowledge of the Recent forms is nearly complete, while that of the extinct forms will always be fragmentary, the Age of Mammals is evidently long since past.

The abundance and great diversity of potential mammal hosts during mid and late Tertiary caution us not to rely too much on the present-day host-relations in attempting to trace the original hosts of the Recent mammal-flies. It can be shown, nevertheless, that the few orders of mammals to which four hippoboscid subfamilies are nowadays restricted, were well represented during the Tertiary, making it at least plausible that each subfamily could have started on hosts similar to those it now prefers or, at any rate, belonging to the same order.

This conclusion is perhaps most probable for the Melophaginae, the only subfamily with a fair number of Recent forms. It now contains 4 genera with 22 valid species, all restricted to the suborder Ruminantia (in which Simpson unites the Pecora and Tragulina) in the order Artiodactyla, and is world-wide, though more abundant in the Old World. The earliest Artiodactyla definitely recognized as such are of Lower Eocene age; but as they occur both in Europe and North America and have no known relatives in the Paleocene faunae of those regions, they must have been invaders from elsewhere. The original stock of the order was probably derived from more archaic mammals during the Cretaceous, either in Central Asia or, perhaps more probably according to Pilgrim (1941), in Central Africa. The suborder Ruminantia, which alone

concerns us here, presumably had a common ancestor in late Eocene, and flourished with a world-wide extension during the Oligocene and Miocene. Although it declined during the Pliocene, it is even now incomparably the most widespread and most differentiated group of Artiodactyla.

The early history of the Tragulina is somewhat confused, but the only Recent family, Tragulidae, has been traced as far back as the Upper Miocene in Europe and Asia; it was never very prolific and survived only in 2 genera with a few species in Africa and Asia. The scarcity and restricted areas of the Recent species no doubt explain why only one fly (*Lipoptena gracilis*) is known from the Tragulina (namely the Oriental *Tragulus*).

Of the other Melophaginae, 20 parasitize Pecora of the families Cervidae and Bovidae (Part I, pp. 287-294), the host of one (*Lipoptena grahami*) being as yet unknown. These keds are about equally divided between the two families (2 genera with 9 species on Cervidae; 3 genera with 11 species on Bovidae); but they are more numerous in the Old World (3 genera with 16 species) than in the New (2 genera with 4 species). No species is known to occur on both families. The original birthplace of the Pecora seems to have been Central Asia, probably during the Oligocene. They became a flourishing group, spreading to all parts of the world except Australia, Tasmania, New Zealand, the Pacific Islands (including Hawaii), Madagascar and the Antilles.

Primitive Cervidae are found in the Oligocene and Miocene of Central Asia, Europe and North America; but the modern types, to which the Recent genera belong, are not known from before the Pliocene in the Old World and the Pleistocene in the New. Presumably the ancestors of all the Recent American Cervidae migrated from the Old World well along in the Pliocene (Simpson, 1945, p. 268). This late arrival possibly accounts for the paucity of native American mammal-flies, the known 4 species being restricted to 3 genera of Cervidae (*Odocoileus*, *Mazama* and *Ozotoceras*), all of the subfamily Odocoileinae. The 5 Melophaginae of Old World Cervidae have a greater variety of hosts, being known from 6 genera in the 4 subfamilies, Moschinae (*Moschus*), Muntiacinae (*Muntiacus*), Cervinae (*Cervus* and *Axis*), and Odocoileinae (*Capreolus* and *Alces*). All the keds of Cervidae (8 *Lipoptena* and 1 *Neolipoptena*) belong to the more generalized tribe Lipoptenini.

The strictly North American Antilocapridae, or pronghorn antelopes, abundant during the Pliocene, comprise only one Recent

genus and species. The few sporadic records from the pronghorn of *Neolipoptena ferrisi*, a regular parasite of Cervidae (*Odocoileus*) are probably due to accidental straggling from deer. In any case, they are of no particular significance for the present discussion.

True Bovidae are recognized as far back as the Lower Miocene in the Old World; but in the New World they appear first in the Pleistocene, evidently following an invasion from Eurasia. In the Recent American fauna they are represented only by *Oreamnos*, *Ovibos* and *Ovis*, in the subfamily Caprinae, and by *Bison*, in the subfamily Bovinae. The late arrival and scarcity of Bovidae in the New World, as well as their restriction to temperate North America, probably account for the American Recent species having no known hippoboscids. All 5 subfamilies of Bovidae recognized by Simpson (see Part I, pp. 289-293) contain regular breeding hosts of Melophaginae in the Old World. The Bovinae date from the Lower Miocene, the Hippotraginae, Antilopinae and Caprinae from the Lower Pliocene, and the Cephalophinae from the Pleistocene. It seems possible therefore that the ancestors of some of the less specialized Lipoptenini passed to Bovinae during the Miocene; while the very specialized, degenerated Melophagini, now restricted to 3 genera of Caprinae (*Capra*, *Ovis*, and *Rupicapra*), probably developed later, perhaps during the Pliocene.

From the evidence presented in the foregoing paragraphs it seems fairly certain that the ancestral stock of all Melophaginae originated in the Old World during the Miocene, perhaps first on Cervidae, passing later to Bovidae. It migrated with Cervidae to the New World during the Pliocene, after *Lipoptena* had acquired its modern generic characters. To judge from the great reduction of the abdominal sclerites, the strictly American *Neolipoptena* is more specialized and probably evolved in the New World during the Pliocene from a *Lipoptena*-like ancestor.

The Hippoboscinae comprise 8 Old World species of *Hippobosca* (J. Bequaert, 1931, 1939*b*, and 1941*a*). The 4 species known from wild hosts are strictly African: *H. rufipes* of antelopes, also established on domesticated equines and bovines; *H. hirsuta* and *H. fulva* of antelopes; and *H. struthionis* of the ostrich. *H. camelina*, of northern Africa and southwestern Asia, occurs nowadays only on domesticated camels and dromedaries; it was presumably retained without change from wild camel ancestors. *H. equina* and *H. variegata* are more difficult to deal with, as they are found only on domestic equines and bovines, being almost equally common on

both. Their present distribution in domestication is extensive and includes some African territory; but much of it is artificial and due to the agency of Man. What the original hosts and habitat were is at present an insoluble problem (Part I, pp. 301-308). I assume tentatively that *H. equina* was a parasite of both wild equines and bovines when these animals were first domesticated, leaving open the question of its original wild host. This may have been one of the African Bovidae (Artiodactyla), from which it passed in nature to wild equines before domestication was attempted. *H. variegata* was almost certainly parasitic of one of the putative ancestors of cattle, either in Africa or in southern Asia, passing later to domestic equines. *H. longipennis*, a common fly of wild African Carnivora, spread with domestic dogs to many parts of the Old World (Part I, pp. 298-301). Almost certainly it evolved rather recently (perhaps during the Pleistocene) from *H. equina*, to which it is so close that it is sometimes regarded as at best subspecifically distinct. *H. struthionis* is specific of the African ostrich and its ancestor perhaps lived on antelopes in the same area. Ostriches are flightless, swiftly running birds, ecologically similar to antelopes, with which they associate sometimes in common herds.

The foregoing data seem to indicate that the evolution of the Hippoboscinae, like that of the Melophaginae, was closely tied up with the rise and decline of the Artiodactyla, particularly of the suborder Ruminantia. This is fairly certain for *H. rufipes*, *H. hirsuta*, *H. fulva*, *H. equina*, and *H. variegata*; also for *H. camelina*, as the Camelidae are the only Recent survivors of the suborder Tylopoda in the Artiodactyla. Camelidae are known in the New World as far back as the Upper Eocene; but in the Old World they appear only in the Pleistocene and apparently were never very numerous. Their early history, however, possibly has little bearing on the evolution of *Hippobosca*, as *H. camelina* may have evolved from a congener living on one of the Ruminantia. In view of their distinctiveness, it seems reasonable to assume that the Hippoboscinae once contained many more African species, chiefly parasites of Ruminantia. *H. struthionis* likewise was presumably derived from a louse-fly of Ruminantia, most probably of antelopes. The Struthionidae first appear in the Lower Pliocene of Asia and southern Europe; but in Africa they are not known with certainty before the Lower Pleistocene (Howard, 1950, p. 18). The origin of *H. struthionis* could then be dated tentatively from the Pleistocene, when the African Bovidae were seemingly at their

peak. It should be noted that all known species of *Hippobosca* are very similar and that their specific characters show no obvious adaptations to the present-day preferred hosts. This is particularly true of *H. struthionis*, which possesses no peculiarity that would seem to fit it specifically to life in plumage rather than in pelt.²¹

Allobosca crassipes, the single species of Alloboscinae, occurs only in Madagascar as a specific parasite of Lemuridae and Indridae. These Primates of the superfamily Lemuroidea are likewise restricted to Madagascar and the Comoros in the Recent fauna (Simpson, 1945, pp. 61-62). Lemuroidea of extinct families are known from the Paleocene and Eocene of Europe and North America; but in Madagascar they have been found fossil only in Pleistocene deposits. In view of the former wide range of the superfamily, it would seem most hazardous to assume that the ancestor of *Allobosca* originated in Madagascar from a bird-fly that passed to early lemurs or indrids, though this is not impossible. Some of the specializations of the legs, frons, antennae and wings of *Allobosca* are perhaps special adaptations to life on lemurs; but too little is known of this fly to speculate upon the matter.

The Ortholfersiinae or wallaby-flies of Australia and Tasmania are the least studied of all louse-flies. Apart from their being restricted to Marsupialia of the superfamily Phalangeroidea and to the family Macropodidae, almost nothing is known of their habits. All reliable host records thus far are from members of the subfamily Macropodinae. The Macropodidae are nowadays endemic in the Australian area and they are known as fossils only from the Australian Pleistocene. That the order Marsupialia can be traced outside Australia as far back as the Upper Cretaceous has probably no bearing on the origin of the Ortholfersiinae. Being restricted to the Macropodinae, the wallaby-flies may have originated in the Australian area from bird-flies that passed to ancient wallabies. They seem to have departed less than other mammal-flies from the original bird-fly type, suggesting that they are perhaps of more recent origin. Further surmises would be futile, as the "recorded history of marsupials is very defective because of the almost complete ignorance of Tertiary Australian forms" (Simpson, 1945, p. 171).

²¹ The information on the Artiodactyla used in discussing the evolution of the Melophaginae and Hippoboscinae was obtained from Simpson (1945, pp. 143-162 and 258-272).

ENTOMOLOGICA AMERICANA

V. ORIGIN AND SUGGESTED PHYLOGENY

Throughout my discussion of hippoboscoid evolution I stressed that the factual evidence is fragmentary and inconclusive, chiefly owing to the scant fossil record and the small number of Recent genera and species, clearly remnants only of a once more varied group. Nevertheless, some tentative conclusions possibly of more general interest may be drawn from the foregoing sections.

1. **Basic Hippoboscoid Features.** To the student of evolution the hippoboscids appear as integral ectoparasites successfully adapted in structure, function and behavior to permanent adult life on birds or mammals, to a strict blood diet and to a very low rate of reproduction by adenotrophic viviparity. Each of these three lines of adaptation involved many structural and physiological departures from the more primitive, free-living, polyphagous and oviparous dipteran ancestors. Not the least interesting aspect of this evolutionary process is that the final product is a closely integrated harmonious whole, one of the most intricately perfect in the animal kingdom.

a. The basic structural peculiarities of all hippoboscids, namely the flattened body, wedge-shaped head, modified antennae and widened sternal area, now function as adaptations or adjustments to permanent, obligate ectoparasitism. They are, however, so universal and so uniform throughout the family, that they must be of great antiquity and possibly were acquired in some less specialized form by the hypothetical Proto-Hippoboscidae before the flies became permanently established on the hosts. It is by no means clear what circumstances determined the original trends for such far-reaching changes, eventually all coördinated toward a common goal. On the modern assumption that Natural Selection works on small mutations produced at random, there seems to be scarcely sufficient selective power in a shift from free-living conditions to permanency on a bird or a mammal.

Indeed, a comparison of the Glossinidae and Hippoboscidae makes one wonder whether permanent ectoparasitism offers decisive advantages over free life. In discussing the relationship between the two families I pointed out that they share the exclusive blood diet at all stages and the adenotrophic viviparity, but differ fundamentally in body structure. The free-living Glossinidae are only slightly more specialized higher Muscoidea. They stalk the vertebrates on which they feed and keep on the alert while engorging as quickly and as fully as possible. Their sense organs, par-

ticularly of sight and smell, are unusually keen, their flight responses rapid and their oesophageal diverticulum is filled to capacity at the end of a meal. When fully engorged, they are helpless and hide or rest while digesting. They are exposed to many hazards, to which they often succumb. The lack of permanent shelter and the need for proper temperature and humidity, especially in connection with adenotrophic viviparity, limit their present-day occurrence to the tropics. On the other hand, they can move freely among a variety of hosts and environments, retain much latitude in the choice of the food supply, and are able to withstand protracted fasting. These advantages enable them to survive on cold-blooded as well as on warm-blooded hosts and to become adapted to a wide range of ecological conditions. It is significant that, when undisturbed by Man, their populations are much larger than those of most louse-flies, in spite of a similar low rate of reproduction.

In sharp contrast, the Hippoboscidae remain in the plumage or pelt, protected against parasites, predators and adverse climatic conditions, except for brief periods when they leave the host for larviposition, as most of them do (Part I, pp. 116-120). They must, however, be constantly on guard against the host itself, their most effective enemy. As they are permanently settled on the food supply, they can afford to time and limit their meals, so that the diverticulum tends to become functionless. The microclimate of the insulated plumage or pelt offers ideal temperature and humidity for digestion and for viviparous reproduction. Although the louse-flies are essentially tropical, the sheltered environment makes them more independent of the macroclimate, so that some species extend to extra-tropical or even cold-temperate areas with their hosts. Nevertheless, there are some real, though not so obvious, disadvantages to an obligate association with a host. As I have shown in the discussion of the evolution within the family, as host-specificity becomes more restricted it tends to produce an increasing bodily and physiological adaptation to definite types of vertebrates. Much of Part I of this work was devoted to showing that, in spite of their great mobility, a fair proportion of Hippoboscidae are as narrowly host-specific as other groups of ectoparasites. The resulting specializations doom the louse-fly to extinction if its breeding host disappears, a factor no doubt chiefly responsible for the decline of the family at the close of the Tertiary. In most hippoboscids the ability to survive away from the proper host is very limited. In addition, as the majority of species either larviposit

or emerge away from the host, the offspring often fails to reach a suitable host, which explains the small fly populations on individual hosts and the low frequency of infestation most commonly observed (Part I, p. 227).

It is questionable therefore whether the advantages of permanent ectoparasitism outweigh the drawbacks, or, at any rate, have a very high survival value in competitive Natural Selection. It is reasonable to assume that the free-living direct ancestors of the Hippoboscidae first contacted vertebrate hosts for purely trophic reasons, similar to those that attracted other types of free-living hematophagous Diptera. Even some of the latter now tend to remain on the host after feeding. Certain species of Simuliidae, or black-flies, which prefer feeding on birds, are occasionally found fully engorged, hiding in the feathers (J. Bequaert, 1938c, p. 118). The American and European horn-fly *Siphona irritans* (Linnaeus) (= *Lyperosia irritans*; *Haematobia serrata*), an oviparous, blood-sucking muscoid, remotely related to the tsetse-flies and louse-flies, remains almost permanently on cattle which it leaves only for a few minutes to oviposit (Riley and Howard, 1889; McLintock and Depner, 1954). Neither the Simuliidae of birds nor *Siphona* show a noticeable flattening of the body, spreading of the coxae, or other structural adaptations to permanent ectoparasitism. Other non-bloodsucking muscoids, such as *Carnus hemapterus* Nitzsch of Europe and North America and *Neottiophilum praecustum* Meigen of Europe, are also obligate parasites of birds in the adult instar. *Carnus* is of especial interest because the head and thorax are flatter than in its closest free-living relatives and because it loses the wings after settling on the host (J. Bequaert, 1942b).

I suggest that the structures now functioning as adaptations to obligate parasitism did not necessarily start in response to permanency on a host. Some, if not most, of the changes involved may have been initiated before the Proto-Hippoboscidae or the earliest true Hippoboscidae took to remaining on vertebrates. They may even date from a time when the earliest warm-blooded birds were too poorly or too incompletely feathered to offer much shelter to flies. The free-living ancestral forms may have been blood-sucking nidicoles, hiding in or near the nests or nesting sites, in cracks of rocks, beneath bark or among nesting material. The flattening of the body and concomitant changes were in this case at first adaptations to the need for shelter between feedings. Some other dipterous families, such as the Sciaridae, Cypselidae (Sphaeroceridae or Borboridae), Helomyzidae and Phoridae, contain scavengers in

nesses and some of these tend to be depressed. Of course, after the presumed nidicolous ancestors of the louse-flies settled permanently on birds, selection soon enhanced the dorso-ventral flattening because of its obvious advantages on flying hosts.

b. The origin of strict hematophagy and of the adjustments it called for, is not difficult to understand (Part I, pp. 98-99). It seems unnecessary to go into the matter again.

c. In discussing the possible origin of adenotrophic viviparity or so-called pupiparity (Part I, pp. 174-175), I reached the conclusion that it has not been adequately explained thus far. I stress once more that I cannot regard it as a simple improvement upon the ovoviviparity of certain other Diptera, such as those mentioned by Hagan (1951, pp. 80-83). There are no known reproductive arrangements connecting these two types of viviparity in the Diptera. In my opinion, the gap between ordinary ovoviviparity and adenotrophic viviparity is at least as wide as that between the ovoviviparity of certain vertebrates and the placental viviparity of most mammals.

A definite correlation between strict hematophagy and adenotrophic reproduction is sometimes assumed. D.E. Hardy (1954) reported recently that *Prostheochaeta fasciata* Grimshaw, a Hawaiian non-bloodsucking calliphorid, voids a third instar maggot which forms a puparium at once. This raises the possibility that the ancestors of the Glossinidae and Hippoboscidae could have acquired adenotrophic viviparity before they were strictly hematophagous.

The combination of an exclusive blood diet and adenotrophic viviparity results in a highly specialized type of integral parasitism most unusual among insects. The distinction between *partial* and *integral parasitism*, based on the food habits, seems to me more fundamental than any other proposed major grouping of the parasites of vertebrates. It involves not merely adaptive changes in structure and behavior, but also more difficult and far-reaching physiological adjustments of diet and metabolism. Partial parasites have a mixed diet and obtain part of the material and energy they require from a non-vertebrate source, either as adults or more often in the earlier instars. Integral parasites, with a single diet throughout life, derive all material and energy from living vertebrate tissues only.

While integral parasitism is the rule among helminth and arachnid parasites of vertebrates, it is more unusual among insects. Integral insect parasites of vertebrates are of three types. In the

simplest and most frequent type, the adult and all larval instars feed individually on living vertebrate tissue only (Anoplura, Mallophaga, blood-sucking Hemiptera). A second, relatively small group comprises the so-called bot-flies, Diptera which feed in the larval instars on vertebrate tissues only, while the adult takes no food, the mouth-parts being aborted. The so-called "pupiparous" Diptera, namely the Hippoboscidae, Nycteribiidae, Streblidae and Glossinidae, form the third and most select type, in which the adult is strictly hematophagous and the earlier instars are nurtured by the mother fly in the uterus.

2. **Origin of the Family.** It seems well-established that the Hippoboscidae are a specialized offshoot of the diversified muscoid branch of Cyclorrhapha Schizophora. It is also fairly certain that the ancestral Proto-Hippoboscidae were phylogenetically distinct from the ancestors of the Nycteribiidae and Streblidae. The Recent Hippoboscidae appear to be a monophyletic group directly evolved from one type of proto-hippoboscid. There are no clues from which this hypothetical proto-hippoboscid could be reconstructed. The Glossinidae appear to be the closest surviving, collateral relatives of the Hippoboscidae, but are not in the direct line of descent. Presumably both Proto-Glossinidae and Proto-Hippoboscidae arose from the same root of blood-sucking, pupiparous, free-living muscoids. One offshoot of the Proto-Hippoboscidae became an obligate ectoparasite, most probably of birds, and this branch gave rise to the true Hippoboscidae.

3. **Further Evolution in the Family.** The supra-generic divisions or subfamilies recognized in the Recent fauna are the surviving branches of the one ancestral hippoboscid stock. Other similar branches probably were produced at various times, but are now extinct. Of the original branches of bird-flies only two survived, one of them, the Ornithoicinae, retaining more primitive characters than any other subfamily. In the course of time several distinct lineages of bird-flies evolved into mammal-flies, four such phyletic lines being preserved to-day.

Each of the six subfamilies became specialized in its own way, as it tended to be more narrowly adapted to a special type of host. The tendency is most apparent in the mammal-flies, where the Melophaginae are completely, and the Hippoboscinae almost wholly, restricted to Artiodactyla, while the Alloboscinae are specific of Lemuroidea (Primates) and the Ortholfersiinae of Macropodidae (Marsupialia). Either adaptive radiation was more profuse among the Ornithomyiinae of birds and the Melophaginae of mammals

or (more probably) more of the adaptive types survived in these subfamilies. Both now contain besides fully-winged, also subapterous or apterous forms, which are interesting to compare.

It is customary to regard *Melophagus*, the most derivative of the Melophaginae, as the extreme among the specialized hippoboscids. No doubt it is superficially the most aberrant member of the family, looking more like a louse or a tick than a fly. It should be noted, however, that its evolution has been almost entirely regressive, so that it is not much more than a degenerated louse-fly. On the other hand, the subapterous *Myiophthiria*, the most aberrant of the bird-flies, is the final product of a progressive evolution, in which the successive changes resulted not so much in the loss of primitive characters as in refined and specific adjustments to a more complex environment. The fly improved considerably upon its *Ornithomyia*-like ancestor by developing a streamline, spider-like body able to move swiftly and safely among the feathers of aerial birds flying at top speed. Instead of simply losing the wings when they became superfluous or even a hazard, it modified them into short, bristly structures with a dual, tactile and retentive function.

4. **Suggested Phylogeny.** I am averse to drawing up the conventional phyletic outline or "genealogical tree" for any group of animals and particularly so for the Hippoboscidae. Only too often such a graphic presentation, which can at best be only hypothetical, confuses the reader and even its author into mistaking speculation for fact. Even with the best of care, it is scarcely possible to distinguish clearly in such an outline between actual observations, which can be controlled, and interpolated surmises, which cannot. For these reasons I shall only summarize the facts and assumptions presented in the foregoing pages, in what I conceive to be the broad lines of the past evolution of the louse-flies.

Speiser (1908c, pp. 440-446) made, so far as I know, the only previous attempt at a phylogeny of these insects, for which he drew up two genealogical schemes, one for the genera and the other for the subfamilies. Some of his suggestions are most valuable and I have mentioned them in my own work. His supra-generic classification (p. 445) differs, however, in many respects from my own. Although he pointed out the primitiveness of *Ornithoica*, he failed to give it proper recognition. He also overlooked the isolated position of the Ortholfersiinae, which he merged in his unnatural group Olfersiinae. His genealogy of the genera (p. 442) is based on the premise that Recent genera evolved from other Recent genera, a point of view with which I disagree. Moreover, some of the de-

tails of his scheme are most improbable. *Ornithophila*, which he derives from the *Ornithomyia* stock, is only *Lynchia* with preserved ocelli. *Stilbometopa* is more closely related to *Ornithoc-tona* than to *Crataerina* or *Myiophthiria*, near which he places it. *Myiophthiria*, *Crataerina* and *Stenepteryx* have many features in common and should have been grouped together.²²

If it is agreed that the Glossinidae and the Hippoboscidae had most probably as common ancestor a primitive type of free-living, blood-sucking, pupiparous muscoid, this ancestral stock must have been extremely ancient. It may have appeared in the early Mesozoic, developing in association with terrestrial vertebrates even before the earliest birds evolved. Some time during the Cretaceous, when the birds were differentiating actively, the stage was set for the separation between the Proto-Glossinidae and the Proto-Hippoboscidae. The latter were at first closely associated with the nesting sites of the birds, on which they fed temporarily. The need for hiding places between meals resulted in a tendency toward flattening the body. This trend became more pronounced, particularly on the head and the sternum, as the association with birds became more permanent. It had a decided selective value when the flies were induced to take advantage of the shelter offered by the plumage. In view of the positive fact that the one known fossil hippoboscoid of the Oligocene is as typical and as specialized as most Recent bird-flies, the primitive true hippoboscids must be considerably older. Possibly they evolved during the Paleocene or early Eocene, as moderately flattened, obligate ectoparasites, with simple claws, a straight anterior thoracic margin, large abdominal sclerites, and fully-developed wings with a venation perhaps even more complete than that of *Ornithoica* or *Ornithomyia*.

The Oligocene bird-fly belongs definitely to the Recent subfamily Ornithomyiinae (with split claws and prominent humeral callosities) and to the recent genus *Lynchia* (with reduced wing venation and reduced abdominal sclerites). It was therefore a fairly specialized fly. On the other hand, all Recent mammal-flies have retained the primitive simple claws and most of them lack prominent humeral callosities. It seems therefore reasonable to assume that the splitting of the original hippoboscoid stock into several

²² In using Speiser's genealogy of the genera, the reader should keep in mind that his *Olfersia* is now *Lynchia*; his *Lynchia* now *Pseudolynchia*, and his *Pseudolfersia* now *Olfersia*; his *Icosta* is now united with *Lynchia*.

branches (subfamilies, tribes and genera) occurred during the latter half of the Eocene. In particular, the shift from birds to mammals most probably occurred during the Eocene, when the evolution of mammals was most active.

Although the fossil record can never be more than fragmentary, that of the mammals is much more complete than that of almost all other animals. In the groups of mammals where it is best known, the genealogy often appears as a repeated and intricate splitting, resembling a bush rather than a tree. The Recent forms then represent the last surviving twigs on some of the side branches, other branches having become extinct before the Recent era. (See for instance, Simpson, 1953, p. 260, for the genealogy of the Equidae). Where so much of the evolution of the Hippoboscidae ran parallel with that of the mammals, it seems logical to assume that the unknown genealogy of these flies was of the same "bushy" type. Probably about the middle of the Eocene, the primitive, bird-inhabiting hippoboscids produced several more or less specialized branches, some remaining on birds, others shifting to mammals. By the early Oligocene, the Recent subfamilies and genera were all in existence, essentially as we know them to-day. Several, perhaps many, other similar branches appeared, but did not survive. As there are no Eocene fossils from which any of the immediate ancestors of the Recent hippoboscids could be surmised, it seems utterly futile to search for more definite relationships between the few surviving Recent genera and supra-generic groups.

REVISION OF AMERICAN GENERA AND SPECIES

Excluded Genera. The following genera, listed sometimes from the New World, are neither autochthonous there nor well-established introductions by Man.

Hippobosca Linnaeus (1758). There is no real evidence that this Old World genus ever became naturalized in the New World on either a domestic or a wild host. *H. equina* Linnaeus, a common parasite of cattle and horses (Part I, p. 304), was mentioned by W. Kirby (1837, *Fauna Boreali-Americana*, **4**, p. 317; reprinted by Bethune, 1881, *Canad. Entom.*, **13**, p. 169), with a rather fanciful description, but without definite locality.²³ Linnaeus (1758,

²³ Kirby says, for instance: "One of the characters assigned to this genus by Fabricius is the want of stemmata, but if the present species is examined under a powerful magnifier, one will be discovered at the posterior internal angle of each eye." No species of *Hippobosca* has even traces of ocelli. Kirby must have seen the pits left by the vertical bristles, after these were broken.

1, p. 607) originally gave both Europe and North America as the habitat of his *H. equina*, but this can scarcely be used as evidence that the fly occurred in the New World at his time. Fabricius (1775, *Syst. Ent.*, p. 803; 1805, *Syst. Antliat.*, p. 337) merely repeated Linnaeus. H. Loew (1864, *Amer. Jl. Sci.*, (2), **37**, p. 518) included the fly in his list of Diptera common to North America and Europe, no doubt on Linnaeus' and Fabricius' authority. B. D. Walsh (1864, *Proc. Ent. Soc. Philadelphia*, **3**, p. 216) and Osten Sacken (1858, p. 86; 1878, p. 214) also copied the earlier authors. None of these writers cited a definite American locality. Asa Fitch (1850, p. 797) first cast doubt on the supposed occurrence of *H. equina* in North America.²⁴ Although Aldrich (1905, p. 653) made a similar statement, Speiser (1907b, p. 103; 1908c, p. 303) listed it again as a North American hippoboscid. Dr. F.C. Bishopp informs me (*in litt.*, 1945) that, in his long experience with parasitic Diptera of domestic animals, he never saw a *H. equina* taken in North America. The only American *equina* I have seen myself was received from Dr. H. de Souza Lopes, of the Instituto Oswaldo Cruz, labelled as taken by J. Moussatali at Rio de Janeiro, in May, 1948, on a cow recently imported from Holland. Such accidental, but temporary importations must have occurred from time to time with horses or cattle.

Hippobosca variegata Megerle von Mühlfeld (1803). This species, more often called *Hippobosca maculata* Leach (1817), is common on domestic cattle and equines, and rare on camels, in the tropical and subtropical parts of the Old World (Part I, p. 305). *Hippobosca fossulata* Macquart (1843, p. 433 [p. 276 of reprint]), another synonym of *H. variegata*, was described, without mention of sex or host, from "Brazil or Chile." The type, seen at the Paris Museum in September, 1951, is a typical *H. variegata*. Speiser (1904a, p. 333) recognized Macquart's *H. fossulata* in a specimen at the Vienna Museum, labelled as taken in Surinam by Thorey in 1859; but later (1908c, p. 421) he cited it from Colombia, probably by oversight. If Macquart's and Speiser's localities are reliable, these old American specimens no doubt came from freshly-imported horses or cattle, as was the case of the Brazilian *H. equina* mentioned above. At any rate, there is no evidence that *H. variegata* is now established anywhere in tropical America. I reported (1951b, p. 49) a dead specimen found at Miami, Florida, July 19,

²⁴ Fitch wrote "I am not aware that it has ever been discovered on this side of the Atlantic."

1944, on a plane arriving from Casa Blanca, Morocco, by way of Bermuda.

I recorded (1931, p. 315) a specimen of *Hippobosca longipennis* Fabricius (= *H. capensis* v. Olfers; *H. francilloni* Leach; *H. canina* Rondani), in the Canadian National Collection, labelled "Okanagan Falls, British Columbia, May 20, 1913 (E.M. Anderson)," without indication of a host. If this fly was actually taken in British Columbia, it came probably from a dog newly arrived from the Far East, where the species is a common pest (Part I, p. 299).

Hippobosca camelina Leach (= *H. dromedarina* Rondani; *H. bactriana* Speiser) is normally a parasite of camels and dromedaries in the Old World (Part I, pp. 308-309). I mentioned in a previous section a specimen found dead on a plane arriving in New York. Another, at the U. S. National Museum, is labelled as taken July 3, 1925, at Athenia, New Jersey, on a recently imported camel.

Ornitheza Speiser (1902) is restricted to the Old World. In his "Catalogue of North American Diptera" (1905, p. 654), Aldrich included *Ornithomyia butalis* Coquillett (1899a, p. 346; no sex; Bering I.; on "*Butalis sibirica*" [= *Muscicapa sibirica*]). He later (1923, p. 78) transferred this fly correctly to the genus *Ornitheza*. Bering I., one of the Commander Group, lies a short distance off the east coast of Kamchatka and must be considered part of Asia. A recent study of Coquillett's type, a female at the U. S. National Museum, shows that *O. butalis* is a synonym of *Ornitheza metallica* (Schiner), widely distributed in the Old World on a variety of hosts, but unknown from the Americas (Part I, p. 324).

Melophagus is not native of the Americas; but the sheep-keed, *M. ovinus*, was introduced by Man soon after Columbus' time.

1. SUBFAMILY ORNITHOICINAE

Ornithoica Rondani, 1878

Ornithoica Rondani, 1878, Ann. Mus. Civ. Stor. Nat. Genova, **12**, p. 159 (monotypic for *Ornithoica beccariina* Rondani, 1878 = *Ornithomyia confluenta* Say, 1823).

Ornithoica Mik, 1891, Wien. Entom. Zeitg., **10**, p. 250 (emendation of *Ornithoica*; same type).

Ornithoica Speiser, 1908, Zeitschr. Wiss. Insektenbiol., **4**, p. 442 (error for *Ornithoica*).

Ornithocira Ferris, 1926, Sarawak Mus. Jl., **3**, pt. 3, p. 280 (in the combination *Ornithocira beccariina*; error for *Ornithoica*).

Ornithoecia Lameere, 1938, Précis de Zoologie, **5**, p. 145 (error for *Ornithoica*).

Anthoica "Rond." Coquillett, 1899, Canad. Entom., **31**, p. 335 (with characters; monotypic for *Ornithomyia confluenta* Say; error for *Ornithoica*, corrected on p. 343). Not *Anthoica* Rondani, 1861.

Generic Characters. Small, rather robust, moderately flattened, fully-winged parasites of birds, not metallic-greenish, without dull-green pigment in the haemolymph. Head (Figs. 24*F'* and 25*C*) moderately depressed, transversely elliptical, nearly free from anterior margin of prescutum, which is scarcely or not covered by the occiput. Ocelli present, well developed. Eyes large, covering the sides of the face and extending partly over the under side. Upper orbit distinct. Postvertex and frons far apart; intervening medio-vertex much longer than either. Upper end of inner orbit produced into a short, erect tubercle or lobe bearing the vertical bristle; this tubercle is usually flattened and difficult to see in flies mounted on slides. Occipital margin straight. Frons (Fig. 24*G*, corrected from Fig. 5*C*, where the lunula was omitted) much shorter than vertex; upper, visible portion consisting mostly of the lunula, below which a single pit is filled by the antennae; interantennal area (frontal carina) of other Hippoboscidae barely indicated by a very short upper crescent, separated from the lunula by an arched impressed line; no apical diverging arms. Antennae (Fig. 24*G*) flattened, moderately developed, slightly diverging, protruding beyond the antennal pit, which is not closed by a rim; 1st segment separated from lunula by a complete suture, setose, elongate, its inner margin touching that of its twin; 2nd segment flattened into a short appendage, broadly rounded-truncate at apex where it bears a few long, curved bristles; protruding arista of 3rd segment flattened, gradually wider and slightly spatulate apically. Palpi moderately long. Thorax (Figs. 23*A-B* and 26*A-B*) moderately depressed. Protergum very short, barely visible from above behind occiput. Humeral callosities broad but short, not appreciably produced forward, broadly rounded off anteriorly; posthumeral suture complete, curving toward anterior margin of prescutum; prothoracic spiracle medium-sized, mostly dorsal at curved edge of outer margin. Antero-median area of prescutum slanting forward, with nearly straight post-occipital margin; transverse mesonotal suture before hind third of mesonotum, broadly interrupted over median half, deep laterally; postalar callus set off by a slight groove from disk of mesoscutum; no visible median notal suture; notopleuron wedge-shaped, much narrowed anteriorly, set off by a complete, deep suture from prescutum. Dorsal portion of anepisternum wide, lathe-shaped, with broadly rounded, scarcely projecting outer hind edge. Scutellum large, about twice as wide as long, lozenge-shaped, with rounded, low anterior and posterior angles, and narrower, more triangular sides; surface even, nearly flat; scuto-scutellar suture deep. Subscutellum

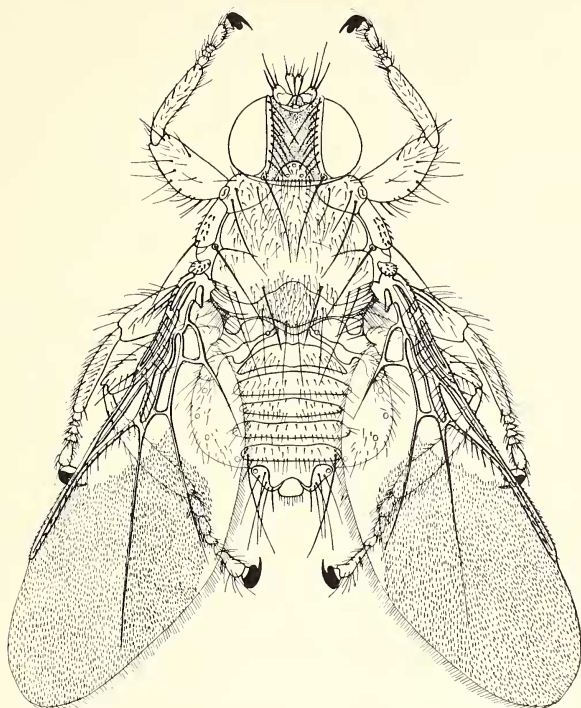


Fig. 22. *Ornithoica vicina* (Walker), ♀, Colorado Springs, on *Pica pica hudsonia*. × about 20.

narrowly visible from above behind hind angle of scutellum. Pleurotergite slightly swollen, without process. Sternum (Fig. 12B): pro-mesosternal suture developed only in the middle; prosternum a single, broad, trapezoidal sclerite; no sclerite in front of it in the cervical membrane; mesosternum apparently a single sclerite, with a median sternal suture over its entire length, a very slight depression without true suture setting off a triangular area near each mid coxa (? rudimentary furcasternum); metasternum undivided, consisting of a large, wedge-shaped combined basisternum and furcasternum, also divided throughout by a median sternal suture, followed by a short undivided sclerite (? spinasternum); no metasternal spur near hind coxa; pleural areas partly visible from below at sides of sternum proper. Sides of thorax more convex than usual in the family, only slightly hollowed out anteriorly for the fore femora. Metathoracic spiracle placed as in *Ornithoetona*. Legs (Fig. 23A)

moderately long and robust; femora slightly swollen, fore femora somewhat more so; tibiae flattened; segments of fore and mid tarsi short and broad, those of hind tarsi more elongate; hind basitarsus only slightly lengthened, without transverse row of stiff setae beneath; tips of all tibiae normal; tibial spur strong on fore and mid legs; on hind legs not differentiated from the several apical bristles. Claw (Fig. 24E) ending in a long, sharp, single tooth, but appearing bidentate owing to the heavy, blunt basal "heel." Wing (Figs. 24A-B and 25A-B) fully developed and functional; venation complete for the family, including three cross-veins, differing from that of *Ornithomyia* only in the peculiar 3rd longitudinal vein: this is bent upward beyond anterior cross-vein, its apical portion running close to and parallel with costa; a reclining costal spine at tip of subcosta; costa beyond this very weak or seemingly interrupted as far as apex of 1st longitudinal; subcosta complete, ending in costa; bullae in anterior basal cross-vein and in basal elbow of 4th longitudinal; costa setulose; a row of long or short setae over entire length of 1st and 3rd longitudinals on both sides of wing; membrane partly covered with microtrichia on both surfaces; alula well developed, fringed with long setae; hind margin of wing from base to tip fringed with fine, short hairs; both calypteres rudimentary. Abdomen of female (Figs. 23A and 26A) dorsally with 5 large, transverse median sclerites, the 5th sometimes contracted medially; median tergites covering most of the dorsum in newly-emerged, unfed, non-gravid flies, but disconnected by membranous areas when the abdomen is distended; two basal laterotergites, one on each side, often more or less fused with the basal median tergite, and followed on each side by a second, smaller and usually less sclerotized laterotergite; apically on each side a small sclerite, partly dorsal, partly ventral; ventrally a basal, elliptical median sternite and a median pair of small, setigerous preapical plates. In the male (Figs. 23B and 26B), the arrangement of the sclerites is much the same; but there are only four complete median tergites, usually larger than those of the female, followed by a pair of apical sclerites sometimes joined medially, and the ventral preapical plates are very small. Seven pairs of abdominal spiracles, placed somewhat differently in both sexes, as shown in Figs. 23A-B. Male terminalia very simplified: gonocoxites (paralobes) nearly aborted, reduced to two minute, soft protuberances (even more reduced than in *Ornithomyia*) bearing 2 short setae, placed some distance from the sides of the horseshoe-shaped sclerite; penis valves (parameres) sharply pointed, straight; penis rod-like, very slender apically. Body rather densely setose, particularly on the thorax. On head, orbital

bristles few, in one or more irregular rows; postvertex with several short setae, irregularly scattered; one long vertical bristle on each side on a raised lobe; 4 long bristles (2 anterior, 2 posterior) on each of the lateral sclerites of gula. On thorax, disk of mesonotum and scutellum mostly covered with many short, soft setae; the setae very short and spiniform on humeral callosity and anepisternum; in addition: 3 or 4 humerals, 2 very long; 1 very long posterior notopleural, the notopleuron otherwise bare; 1 very long mesopleural at outer hind edge of anepisternum; 2 or 3 postalars; 1 posterior dorso-central, close to scuto-scutellar suture; usually 2 pairs of very long preapical scutellars, one medially, the other in outer corners, occasionally a third shorter bristle between them on one or on both sides. Sternum with many scattered short setae and sometimes a few longer bristles on meso-basisternum; prosternum bare; meta-thoracic pleurotergite with a prominent, subvertical, dense row of long bristles. Abdomen dorsally mostly bare on the soft areas, except at the sides which have a few short setae on thickened bases; basal median tergites with many scattered short setae; succeeding tergites with fewer short setae, mostly in an irregular preapical row, some of the lateral setae longer, particularly on 5th tergite; apical sclerites with 4 or 5 very long bristles. Ventrally, female with conspicuous short, spine-like or hook-like setae on strong, knob-like swellings, the number and arrangement differing in the several species, and in addition with a few short, soft setae more or less in transverse rows and some longer bristles on the apical sclerites; venter of male usually with only normal, long setae, but with setigerous tubercles in *O. unicolor* Speiser and *O. philippinensis* Ferris, both of the Old World. Legs moderately bristly; hind trochanters with only soft setae in female (Fig. 24C), in addition with short, spine-like bristles near the outer hind margin in male (Fig. 24D).

Ornithoica is cosmopolitan throughout the tropics and subtropics. It occurs on a variety of birds, mainly Passeriformes, Strigiformes and Ciconiiformes, most species showing little host specificity. In Europe, *O. turdi* has been taken as far north as 46° N., and in America, *O. vicina* extends to 50° N. The genus contains few species, the exact number being uncertain, but probably 6 or 7. Of the 2 American species, *O. confluenta* is native in the Old World also, while *O. vicina* is possibly identical with the Old World *O. turdi*.

Key to American Species of *Ornithoica*

1. Wing membrane with microtrichia on upper and under sides over apical two-thirds to three-fourths, including more than apical half of 3rd posterior cell, extreme tip of axillary cell,

and narrow area of 2nd basal cell. Interocular face at mid-height as wide as or slightly narrower than an eye in both sexes. Abdomen of female dorsally with a lateral patch of long setae close to and basad of the paired preapical tergal plates *O. confluenta*

Wing membrane with microtrichia on upper and under sides over slightly more than apical half, including a narrow anterior patch in apical fourth to third of 3rd posterior cell (axillary and 2nd basal cells entirely bare). Interocular face at mid-height wider than an eye in female, about as wide as an eye or slightly wider in male. Abdomen of female with very few, short dorso-lateral setae close to the paired preapical tergal plates *O. vicina*

Ornithoica vicina (Walker)

Figs. 5C, 12B, 22, 23A-G, and 24A-G

- Ornithomyia vicina* Walker, 1849, List Dipt. Brit. Mus., 4, p. 1144 (no sex. Jamaica: on "*Ephialtes grammicus*" [*Pseudoscops grammicus*]. Type ♂ at Brit. Mus.). Osten Sacken, 1858, Cat. Dipt. North America, p. 86; 1878, Smithson. Misc. Coll., No. 270, p. 213. Johnson, 1894, Proc. Ac. Nat. Sci. Philadelphia, p. 281. Lutz, Neiva and da Costa Lima, 1915, Mem. Inst. Osw. Cruz, 7, p. 190 (copy of original description).
- Ornithoica vicina* Austen, 1903, Ann. Mag. Nat. Hist., (7), 12, p. 263 (type. Also Jamaica: on *Amazona* ["*Psittacus*"] *l. leucocephala*). Ferris, 1929, Canad. Entom., 61, p. 285. J. Bequaert, 1940, Mem. Soc. Cubana Hist. Nat., 14, p. 327; 1940, Rev. Acad. Colombiana Cienc. Ex. Fis. Nat., 3, No. 12, p. 416; 1941, Occ. Papers Bernice P. Bishop Mus., Honolulu, 16, No. 11, p. 289; 1942, Bol. Entom. Venezolana, 1, No. 4, p. 83; 1943, Jl. of Parasitology, 29, p. 131. Stuardo 1946, Catálogo Dípteros Chile, p. 187. Bartlett, 1947, The Auk, 44, p. 457 (Massachusetts: Amherst, on *Otus asio naevius*). Anduze, Pifano and Vogelsang, 1947, Bol. Entom. Venezolana, Num. Extra, p. 6. MacArthur, 1948, Bull. Publ. Mus. Milwaukee, 8, No. 4, p. 394, fig. 236 (Wisconsin: Fox River, Tichigan Marsh, Racine Co., on *Butorides v. virescens*; Cedarburg Swamp, Ozaukee Co., on *Troglodytes aëdon parkmanii*; Dodge Co., off *Turdus m. migratorius*. Illinois: Waukegan, on *Zonotrichia albicollis*; Urbana, on *Buteo jamaicensis borealis*). Alicata, 1948, Rep. Univ. Hawaii Agric. Expt. Sta. for 1946-1948, p. 104 (Hawaii: Honolulu, Oahu I., on *Passer d. domesticus*). Thompson, 1949, Ent. Mo. Mag., 85, p. 248 (Jamaica: Corn Puss Gap, St. Thomas, on *Amazona collaris*). Wray, 1950, Insects North Carolina, 2nd Suppl., p. 33. J. Bequaert, 1951, Agricultura Técnica, Santiago de Chile, 10, pt. 1, (for 1950), p. 9. Campbell and Lee, 1953, Studies on Quail Malaria, New Mexico Dept. Fish Game, pp. 52 and 70 (New Mexico: Las Cruces, on *Lophortyx g. gambelii*); 1953, Completion Report, New Mexico Project W-41-R, p. 3.
- Ornithoetona vicina* Aldrich, 1905, Smithson. Misc. Coll., 46, No. 1444, p. 654.
- Ornithoetona vicina* Gowdey, 1926, Dept. Agric. Jamaica, Ent. Bull. 4, pts. 1-2, p. 89.

- Ornithomyia* sp. near *confluens* Osten Sacken, 1878, Smithson. Misc. Coll., No. 207, p. 263 (California: San José, on "*Accipiter fuscus*").²⁵
- Ornithoica confluens* Aldrich, 1905, Smithson. Misc. Coll., 46, No. 1444, p. 655 (in part); 1923, Insector Insectiae Menstruus, 11, p. 79 (Cuba: Santiago de Cuba. California: Ontario, on *Cinclus mexicanus*.²⁵ Colorado: Hotchkiss, on hawk and owl). E. P. Reed, 1932, Rev. Chilena Hist. Nat., 35, (for 1931), p. 103 (Chile: near Valparaiso). Peters, 1933, Bird-Banding, 4, pp. 71, 72, 73, 74, and 75 (New Hampshire: East Westmoreland, on *Dryobates pubescens medianus*, *Sitta c. carolinensis*, *Dendroica coronata*, *Sciurus n. noveboracensis*, *Spizella p. passerina*, *Melospiza l. lincolni*, *Melospiza g. georgiana*, and *Melospiza m. melodia*; Peterboro, on *Molothrus a. ater*, *Junco h. hyemalis*, *Spizella p. passerina*, and *Melospiza m. melodia*. Massachusetts: Oak Bluffs, on *Penthestes a. atricapillus*, *Quiscalus q. quiscula*, *Molothrus a. ater*, *Pipilo e. erythrophthalmus*, and *Melospiza m. melodia*; Groton, on *Turdus m. migratorius* and *Melospiza m. melodia*; Worcester, on *Hylocichla f. fuscescens* and *Melospiza m. melodia*. New York: Mohawk Lake, on *Turdus m. migratorius* and *Melospiza l. lincolni*; Elmhurst, Long Island, on *Pipilo e. erythrophthalmus*, *Junco h. hyemalis*, *Spizella p. passerina*, and *Zonotrichia albicollis*. Maryland: Silver Spring, on *Cyanocitta c. cristata* and *Junco h. hyemalis*. South Carolina: Summerville, on *Corthylio c. calendula*, *Mniotilta varia*, and *Pipilo erythrophthalmus alleni*. Ohio: Columbus, on *Passerculus sandwichensis savanna*; Gates Mills, on *Spizella p. pusilla* and *Melospiza m. melodia*; Leetonia, on *Spizella p. pusilla* and *Melospiza m. melodia*. Brimley, 1942, Supplement to Insects North Carolina, p. 29 (North Carolina: Raleigh, on *Accipiter cooperii*). Not of Say, 1823.
- Ornithoica confluenta* Speiser, 1902, Termész. Füzetek, 25, p. 334 (new description. Brazil: Rio Grande do Sul); 1907, Ent. News, 18, p. 103 (in part). Lutz, Neiva and da Costa Lima, 1915, Mem. Inst. Osw. Cruz, 7, pp. 187, 188 and 195; Pl. 28, fig. 9 (Brazil: on "*Ramphastos ariel*" [*Ramphastos vitellinus ariel*], *Cyanocorax c. chrysops*, *Troglodytes "musculus wiedi"* [*T. m. musculus*], and *Pitangus sulphuratus maximiliani*). Johnson, 1922, Psyche, 29, p. 80, fig. 1, left hand fig. (Maine: Wilson's Mills, Oxford Co., on *Perisoreus c. canadensis*. California: San José, on "*Accipiter fuscus*." Cuba). Champlain and Knull, 1923, Ent. News, 34, p. 215 (Pennsylvania: Wellsboro, on *Strix v. varia*). Johnson, 1925, Bull. Northeastern Bird-Banding Assoc., 1, p. 52; 1925, Occ. Papers Boston Soc. Nat. Hist., 7, p. 293 (New Hampshire: Peterboro, on *Melospiza m. melodia*. Massachusetts: Braintree, on *Corvus b. brachyrhynchos*). Essig, 1926, Insects Western North America, p. 623, fig. 501. Johnson, 1927, Bull. Boston Soc. Nat. Hist., No. 42, p. 15 (Massachusetts: Wenham, on *Bubo v. virginianus*). Johannsen, 1928, in Leonard, Cornell Univ. Agric. Expt. Sta., Mem. 101, (for 1926), p. 868 (New York: Albany, on *Strix v. varia*). Ferris, 1928, Ent. News, 29, p. 139 (California: Pasadena, infested with mites, *Myialges anchora*). Bau, 1929, Zentralbl. Bakt. Parasit., Abt. 2, 79, pp. 247 and 248 (in part), fig. 2. Johnson, 1929, Bull. Northeastern Bird-Banding Assoc., 5, p. 51 (Massachusetts: Rock, on *Spizella p. passerina*; Wellesley, on *Hedymeles ludovicianus*. New York: Cold Spring Harbor, on *Aegolius a. acadicus*). Ferris, 1929, Canad. Entom., 61, p. 282, figs. 2B, C, E, 3A-B, and 4B (♀ ♂. Massachusetts: Wenham, on *Bubo v. virginianus*; Rock, on

²⁵ The true identity of Osten Sacken's "*Accipiter fuscus*" can not be determined. Aldrich's "*Cypselus mexicanus*" was an oversight for *Cinclus mexicanus*.

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Melospiza m. melodia. California: Bluff Lake, San Bernardino Mts., on *Junco oreganus thurberi*; 1930, Canad. Entom., 62, p. 70 (Panama: Camp Pital, Chiriqui Prov., on *Ramphastos swainsonii*). Johnson, 1930, Publ. Nantucket M. Mitchell Assoc., 3, No. 2, p. 158 (in Nantucket list, but not actually taken there). J. Bequaert, 1933, Rev. Chilena Hist. Nat., 37, p. 165. Dunn, 1934, Psyche, 41, p. 175 (Panama record of Ferris, 1930). Peters, 1936, Bird-Banding, 7, pp. 18, 19, 20, 21, 22, 23, 24, 25, 26, and 27 (New Hampshire: on the hosts listed in 1933 and on *Hylocichla guttata faxoni* and *Geothlypis trichas brachidaetyla*. Vermont: on *Passerculus sandwichensis savanna* and *Melospiza m. melodia*. Massachusetts: on the hosts listed in 1933 and on *Mniotilta varia*, *Quiscalus quiscula aeneus*, *Cyanocitta c. cristata*, and *Spizella p. passerina*. Connecticut: on *Melospiza m. melodia*. New York: on the hosts listed in 1933 and on *Regulus s. satrapa* and *Corthylio c. calendula*. Maryland: on the hosts listed in 1933 and on *Regulus s. satrapa* and *Wilsonia citrina*. South Carolina: on the host listed in 1933 and on *Otus asio naevius* and *Pipilo erythrophthalmus canaster*. Ohio: on the hosts listed in 1933). Herman, 1937, *Op. cit.*, 8, pp. 162 and 165 (New Hampshire: Peterboro, on *Melospiza m. melodia* and *Zonotrichia albicollis*. Massachusetts: North Eastham, on *Tyrannus tyrannus*, *Dumetella carolinensis*, *Dendroica p. pinus*, *Geothlypis trichas brachidaetyla*, *Agelaius p. phoeniceus*, *Molothrus a. ater*, *Pipilo e. erythrophthalmus*, *Passerculus sandwichensis savanna*, *Ammodramus savannarum australis*, *Poocetes g. gramineus*, *Spizella p. passerina*, *Spizella p. pusilla*, *Melospiza g. georgiana*, and *Melospiza m. melodia*.²⁶ Infestation with mites). Spencer, 1938, Proc. Ent. Soc. British Columbia, No. 34, p. 44 (British Columbia: on *Melospiza melodia morphna* and *Cyanocitta s. stelleri*). Procter, 1938, Biol. Surv. Mt. Desert, 6, Insect Fauna, p. 378 (Maine: Mt. Desert, on *Passer d. domesticus*). J. Bequaert, 1939, Science, 89, p. 268. Essig, 1942, College Entomology, p. 814. Augustson, 1942, Bull. So. California Ac. Sci., 40, (for 1941), p. 148 (California: Mono Lake, on *Asio wilsonianus*). Clay and Meinertzhagen, 1943, Parasitology, 35, p. 12 (California: on *Aphelocoma c. californica* and *Pipilo maculatus megalonyx*, each with a Mallophagan, *Brüelia* sp., attached). Herman, 1945, California Fish Game, 31, p. 23, figs. 10B [mislabelled *Lynchia hirsuta*] and 11C. Procter, 1946, Biol. Surv. Mt. Desert, 7, Insect Fauna, p. 437 (Maine: Mt. Desert, on *Passer d. domesticus* and *Turdus m. migratorius*). Not of Say, 1823.

Ornithoeca confluenta Speiser, 1908 Zeitschr. Wiss. Insektenbiol., 4, pp. 203, and 304 (in part).

Ornithoeca promiscua Ferris and Cole, 1922 (June 14), Parasitology, 14, p. 203, figs. 19 and 20A-B (♀. California: Castle Hot Springs, Lake Co., on *Pipilo fuscus carolae*, holotype at California Academy of Sciences, San Francisco; San Francisco, paratype on *Passerella iliaca* subsp.; Pacific Grove, paratype on *Corthylio calendula cineraceus*; King's River, paratype on *Falco s. sparverius*. Two flies, without locality, on *Hylocichla u. ustulata*. Paratypes at Stanford University, Palo Alto, California). Ferris, 1924, Ent. News, 35, p. 235. Essig, 1926, Insects Western North America, p. 621. Ferris, 1927, Canad. Entom., 59, p. 251 (California: Bluff Lake, San Bernardino Mts., on *Junco oreganus thurberi*; Altadena, on *Zonotrichia coronata* and *Pipilo maculatus* subsp. [= *Pipilo maculatus megalonyx*]; Stanford University, on *Zonotrichia coronata*; Pasadena,

²⁶ The North Eastham record from *Zenaidura macroura carolinensis* is here deleted, as suggested by Dr. Herman (see Part I, p. 215). It was repeated by Huff (1939, Jl. Amer. Vet. Med. Assoc., 94, p. 619).

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on *Passer d. domesticus*, *Aphelocoma c. californica*, and *Pipilo maculatus montanus*).

Ornithoica melaleuca Bau, 1922 (October 2), Centralbl. Bakt. Parasit., Abt. 2, 57, pp. 276 and 278 (♀. Cuba: Estacion Meyer, Sa. Clara Province, on "large white owl," surmised by Bau to have been "*Strix flammea furcata*" [*Tyto alba furcata*]. Type presumably at Berlin Museum).

Ornithoica confluenta var. *melaleuca* Bau, 1929, Zentralbl. Bakt. Parasit., Abt. 2, 79, pp. 247 and 248.

Ornithoica species? Bryan, 1921, Proc. Hawaiian Ent. Soc., 4, p. 454 (Hawaiian Is.: Kauai, on pheasant); 1934, *Op. cit.*, 8, pp. 444 and 458. Fullaway, 1932, *Op. cit.*, 8, p. 6. G. B. Thompson, 1938, Ent. Mo. Mag., 74, p. 49.

Distribution and Specimens Examined. DOMINION OF CANADA.

BRITISH COLUMBIA (recorded by Spencer, 1938): Campbell River, Vancouver I., on *Dendragapus obscurus fuliginosus* (C.D. Fowle; the unnamed flies mentioned by Fowle, 1946); Quinsam Lake, Vancouver I., on *Regulus satrapa olivaceus* (J.S.F. Bendell); Duncan, Vancouver I., Oct., on *Junco o. oregonus*; Saanich, on *Aegolius a. acadicus* (G.A.N.); Departure Bay, Nanaimo, 42 specimens on *Otus asio kennicottii* (H.D. Fisher); Cowichan Lake Forest Station, Vancouver I., on *Cyanocitta s. stelleri* (R. Radcliffe); Vancouver, on *Melospiza melodia morphna* (R.A. Cumming) and *Cyanocitta s. stelleri* (G.J. Spencer).—ONTARIO: Toronto, on *Aegolius a. acadicus*, *Zonotrichia albicollis*, and *Junco h. hyemalis*; Lake of Two Rivers, Algonquin Park, on *Melospiza m. melodia* and *Quiscalus quiscula aeneus* (D.M. Davies); Lake Sasajewan, Algonquin Park, on *Melospiza m. melodia* (D.M. Davies); Ottawa, on *Turdus m. migratorius* (J. Fletcher); Arden, Frontenac Co., on *Strix v. varia* (R.O. Lindsay).—QUEBEC: Joliette, on *Asio f. flammeus* (J. Ouellet); St. Anne's, on *Molothrus a. ater* (W.E. Whitehead); Montreal, on *Bubo v. virginianus*, Jan. 3, (Frère Adrien Robert); Rosemont, Montreal, on *Buteo p. platypterus*, Aug. 26 (Frère Adrien Robert).

UNITED STATES. ARIZONA: without more precise locality, 14 flies on *Junco phaeonotus dorsalis* (H.H. Kimball); Williams, Coconino Co., on *Pipilo maculatus montanus* (A.R. Phillips); Phoenix, Maricopa Co., on *Lophortyx g. gambelii* (C. Stannard); Flagstaff, Coconino Co., on *Junco phaeonotus dorsalis*, *Bubo virginianus pallascens*, *Piranga flava hepatica*, *Aphelocoma californica woodhouseii*, and 2 *Turdus migratorius propinquus* (A.R. Phillips); Hualpai Mts., Mohave Co., on *Strix occidentalis lucida* and *Aphelocoma californica woodhouseii* (A.R. Phillips); Sa. Catalina Mts., Pima Co., on *Strix o. occidentalis* (A.R. Phillips); Carter Canyon, Sa. Catalina Mts., Pima Co., on *Troglodytes aëdon parkmanii* (A.R. Phillips).—CALIFORNIA (recorded by Osten Sacken, 1878; Ferris and Cole, 1922; Johnson, 1922; Aldrich, 1923; Ferris, 1927, 1929;

Augustson, 1942; Clay and Meinertzhagen, 1943; Herman, 1945): without precise locality, on *Hylocichla u. ustulata*; Castle Hot Springs, Lake Co., on *Pipilo fuscus carolae* (holotype of *O. promiscua*. — J. Maillard); Woodacre, Marin Co., on *Zonotrichia coronata*; Mono Lake, Mono Co., on *Asio wilsonianus* (R.I. Rutherford); San Mateo Mts., San Mateo Co., on *Strix o. occidentalis* (A.K. Fisher); Berkeley, Alameda Co., on *Passerella iliaca* subsp., Dec. 21, and *Pipilo maculatus falcifer* (H.E. Childs, Jr.), on *Aphelocoma c. californica*, Oct. 20 (S.K. Carnie), and on *Melospiza melodia gouldii*, *Chamaea fasciata phaea* and *Zonotrichia leucophrys nuttalli* (O.E. Sousa); San José, Sa. Clara Co., on “*Accipiter fuscus*” (W. Holden. — In Osten Sacken Coll. at M.C.Z.); Stanford University, Palo Alto, Sa. Clara Co., on *Zonotrichia coronata* and *Otus asio bendirei*; Strawberry, Tuolumne Co., on *Junco oreganus thurberi*, Sept. 16 (W. Jameson); Hastings Reservation near Jamesburg, Monterey Co., on *Pipilo fuscus crissalis* and *Bubo virginianus pacificus* (J.M. Linsdale); Pacific Grove, Monterey Co., on *Corthylio calendula cineraceus* (paratype of *O. promiscua*); Ventura, Ventura Co., on *Buteo jamaicensis calurus*, July 8 (J.M. Robertson); Los Angeles, Los Angeles Co., on *Melospiza melodia cooperi* (P. Stoddard); Altadena, Los Angeles Co., on *Pipilo maculatus megalonyx* (with Mallophagan attached), *Zonotrichia coronata* and *Cyanocitta s. stelleri* (J.E. Law); Pasadena, Los Angeles Co., on *Mimus polyglottos leucopterus*, *Molothrus ater obscurus*, *Euphagus cyanocephalus*, and *Melospiza melodia cooperi* (Josephine Michener), *Carpodacus mexicanus frontalis* (S.F. Wood and Josephine Michener), *Aphelocoma c. californica* (with Mallophagan attached), *Pipilo maculatus montanus*, and *Passer d. domesticus* (H. Michener); Monrovia, Los Angeles Co., on *Tyto alba pratincola* (I. Wilson); Sa. Monica Mts., Westwood, Los Angeles Co., on *Pipilo fuscus senicula* (P. Stoddard) and on *Passerella iliaca* subsp. (H. Graham); Ontario, San Bernardino Co., on *Cinclus mexicanus unicolor*, Aug. 9 (R.E. Snodgrass); Big Bear Lake, San Bernardino Co., on *Junco* sp. (J.E. Law); Bluff Lake, San Bernardino Mts., Riverside Co., on *Junco oreganus thurberi* (J.E. Law); Idyllwild, Riverside Co., on *Cyanocitta stelleri frontalis* (C.L. Remington); King’s River, Fresno Co., on *Falco s. sparverius* (paratype of *O. promiscua*). — COLORADO (recorded by Aldrich, 1923): Hotchkiss, Delta Co., on hawk and owl (T.H. Cowen); Colorado Springs, El Paso Co., on *Pica pica hudsonia* and *Pipilo fuscus mesoleucus* (R.M. Stabler). — CONNECTICUT (recorded by Peters, 1936): Milford, New Haven Co., on *Bubo v. virginianus* (R.C. Morrill); Pomfret, Windham Co., on *Hylocichla f. fuscescens*, Aug. 3; New Haven, New Haven

Co., on *Bubo v. virginianus* (R. Chamberlain). — DISTRICT OF COLUMBIA: on *Aegolius a. acadicus*, Oct. 27 (H.E. Ewing); Woodridge, on *Passer d. domesticus* (E.R. Kalmbach). — ILLINOIS (recorded by MacArthur, 1948): Waukegan, Lake Co., on *Zonotrichia albicollis*, Oct. 6 (W.I. Lyon); Urbana, Champaign Co., on *Buteo jamaicensis borealis* (R. Fautin). — KANSAS: Lawrence, Douglas Co., on *Passer d. domesticus* (C.H. Anderson). — LOUISIANA: Ponchatoula, Tangipahoa Parish, on *Dendrocopos p. pubescens*, Nov. 20 (H.D. Pratt). — MAINE: (recorded by Johnson, 1922; Procter, 1938, 1946): Portland, Cumberland Co., on *Buteo jamaicensis borealis* (A.G. Johnson); Wilsons Mills, Oxford Co., on *Perisoreus c. canadensis* (W.S. Brooks); Mount Desert, Hancock Co., on *Passer d. domesticus* (A.E. Brower); Lincoln, Penobscot Co., on *Bubo v. virginianus* (W.J. Clayton). — MARYLAND (recorded by Peters, 1933, 1936): Beltsville, Prince Georges Co., on *Melospiza m. melodia*, July 8, and *Turdus m. migratorius*, July 23 (P.R. Smith); Laurel, Prince Georges Co., on *Regulus s. satrapa* and *Cyanocitta c. cristata* (E.B. Marshall); Rockville, Montgomery Co., on *Bubo v. virginianus* (C.R. Aschmeyer); Silver Spring, Montgomery Co., on *Passer d. domesticus* (C.M. Herman). — MASSACHUSETTS (recorded by Johnson, 1925, 1927, 1929; Ferris, 1929; Peters, 1933, 1936; Herman, 1937; Bartlett, 1947): Groton, Middlesex Co., on *Mniotilta varia*, *Seiurus a. aurocapillus*, *Cyanocitta c. cristata*, *Melospiza m. melodia*, Aug. 26, *Dendroica a. aestiva*, *Turdus m. migratorius*, *Icterus galbula*, and *Spizella p. passerina* (W.P. Wharton and E.A. Mason); Harvard, Worcester Co., on *Melospiza m. melodia* (J.L. Peters); Amherst, Hampshire Co., on *Otus asio naevius* (L.M. Bartlett); Rock, Plymouth Co., on *Melospiza m. melodia* (A.W. Higgins) and *Spizella p. passerina*; Cohasset, Norfolk Co., on *Melospiza m. melodia*, Aug. 2 (C.L. Whittle); North Eastham, Barnstable Co., on *Poocetes g. gramineus*, *Agelaius p. phoeniceus*, *Melospiza m. melodia*, and *Molothrus a. ater* (C.M. Herman); Athol, Worcester Co.; Wenham, Essex Co., on *Bubo v. virginianus*, Sept. 28 (J.C. Phillips); Cotuit, Barnstable Co., on *Quiscalus quiscula aeneus* (B. Shreve); Milton, Norfolk Co., on *Quiscalus quiscula aeneus* (R.M. Hinchman); Wellesley, Norfolk Co., on *Hedymeles ludovicianus* (Mrs. H.C. Durham); Braintree, Norfolk Co., on *Corvus b. brachyrhynchos*; Chatham, Barnstable Co., on *Butorides v. virescens*, Aug. 10 (J.D. Smith);²⁷ Martha's Vineyard, on *Melo-*

²⁷ It should be emphasized that, although reported as collected on a wader, this fly, as well as the one listed from Tichigan Marsh, Wisconsin, were true *O. vicina*, not *O. confluenta*.

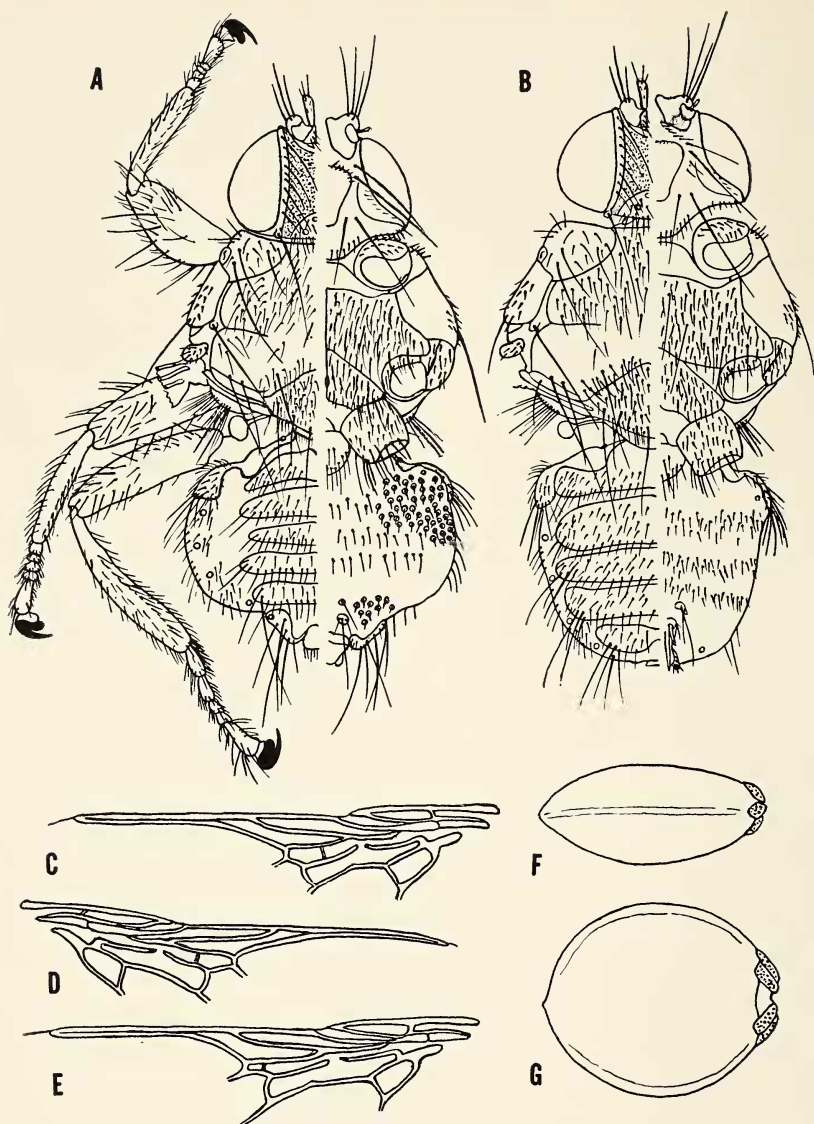


Fig. 23. *Ornithoica vicina* (Walker). A-B, body in dorsal and ventral view: A, ♀, Colorado Springs, on *Pica pica hudsonia*; B, ♂, Sa. Catalina Mts., on *Strix o. occidentalis*. C-E, abnormal venation in 3 ♀, Quinsam Lake, on *Regulus satrapa olivaceus*. F-G, puparium, Wenham, in ear of *Bubo v. virginianus*, from the side (F) and above (G).

spiza m. melodia, *Spizella p. passerina*, and *Agelaius p. phoeniceus* (G.D. Eustis); Oak Bluffs, Dukes Co., on *Cyanocitta c. cristata*, *Melospiza m. melodia*, *Pipilo e. erythrophthalmus*, *Quiscalus q. quiscula*, and *Penthestes a. atricapillus* (G.C. Meleney); Concord, Middlesex Co., on *Melospiza m. melodia* (W.E. Schevill). — MISSOURI: Columbia, Boone Co., on *Asio wilsonianus* (K.C. Rowe). — NEW HAMPSHIRE (recorded by Johnson, 1925; Peters, 1933, 1936; Herman, 1937): Peterboro, Hillsboro Co., on *Melospiza m. melodia*, *Carpodacus p. purpureus*, *Spizella p. passerina*, and *Junco h. hyemalis* (C.L. Whittle); East Westmoreland, Cheshire Co., on *Melospiza l. lincolni*, *Melospiza m. melodia*, *Geothlypis trichas brachidactyla*, *Turdus m. migratorius*, *Seiurus n. noveboracensis*, *Dendroica coronata*, *Spizella p. passerina*, *Dendrocopos pubescens medianus*, and *Sitta c. carolinensis* (L.O. Shelley); Ashland, Grafton Co., on *Melospiza m. melodia* (Mrs. R.B. Harding). — NEW JERSEY: Breeze Hill, Chatham, Morris Co., on *Melospiza m. melodia* (R.D. Connor); Demarest, Bergen Co., on *Toxostoma r. rufum*, *Cyanocitta c. cristata*, *Baeolophus bicolor*, *Turdus m. migratorius*, *Molothrus a. ater*, *Melospiza m. melodia*, *Pipilo e. erythrophthalmus*, *Dumetella carolinensis*, *Hedymeles ludovicianus*, *Icterus galbula*, *Piranga erythromelas*, and *Hylocichla f. fuscescens* (B.S. Bowdish). — NEW MEXICO (recorded by Campbell and Lee, 1953): Las Cruces, Dona Ana Co., on *Lophortyx g. gambelii* (Levon Lee). — NEW YORK (recorded by Johannsen, 1928; Johnson, 1929; Peters, 1933, 1936): Orient, Long Island, on *Pipilo e. erythrophthalmus* (R. Latham); Elmhurst, Long Island, on *Regulus s. satrapa*, *Corthylio c. calendula*, *Junco h. hyemalis*, *Zonotrichia albicollis*, and *Hylocichla guttata faxoni* (Marie V. Beals); Cold Spring Harbor, Long Island, on *Aegolius a. acadicus* (J.M. Andrews); Rensselaerville, Albany Co. (K.W. Cooper); Ellis Hollow, Ithaca, Tompkins Co., on *Bubo v. virginianus* (C.E. Palm) and *Asio f. flammeus* (F. Harper); Caroline, Tompkins Co., on *Bonasa umbellus togata* (E.J. Gerberg); Syracuse, Onondaga Co., on *Spizella p. passerina* (R.D. Manwell); Mohonk Lake, Ulster Co., on *Melospiza l. lincolni*, Sept. 17, and *Turdus m. migratorius*, July 11 (D. Smiley, Jr.); Greenwich, Washington Co. (A. Paladin); Albany. — NORTH CAROLINA (recorded by Brimley, 1942): Raleigh, Wake Co., on *Accipiter cooperii* (Mrs. R.C. Simpson); Hoffman, Richmond Co., on *Bubo v. virginianus* (Mrs. R.C. Simpson). — OHIO (recorded by Peters, 1933, 1936): Gates Mills, Cuyahoga Co., on *Troglodytes a. aëdon*, Aug. 26, *Spizella p. passerina*, *Richmondia c. cardinalis*, and *Molothrus a. ater* (R. Boulton); Leetonia, Columbiana Co., on *Melospiza m. melodia* and

Spizella p. pusilla (H.S. Peters) ; Franklin Co., on *Asio f. flammeus*, Nov. 15 (R.M. Goslin. — The collector noted that the owl had a tree sparrow in the stomach). — OREGON: Portland, Multnomah Co., on *Melospiza l. lincolni*, Sept. 14 (C.M. Gjullin) ; Coburg, Lane Co. (Oregon Agr. Coll.) ; Maupin, Wasco Co., on *Melospiza* sp., Oct. 24 (F.C. Bishopp) ; Sauvies I., Multnomah Co., on *Bubo virginianus saturatus* ; Netarts, Tillamook Co., on *Corthylio calendula cinereus*, Nov. 21, and *Chamaea fasciata phaea*, Nov. 13 (A. Walker). — PENNSYLVANIA (recorded by Champlain and Knull, 1923) : Wilkinsburg, Allegheny Co., on *Hylocichla mustelina* (H.D. Kirk) ; Allegheny Co., on *Asio wilsonianus* (G. Link) ; Mt. Lebanon, Allegheny Co., on *Bubo v. virginianus* (J. Guilday) ; Lester, Delaware Co. (C. Liebeck) ; Wellsboro, Tioga Co. — SOUTH CAROLINA (recorded by Peters, 1933, 1936) : Summerville, Dorchester Co., on *Otus a. asio*, Sept. 26 (G.R. Lunz, Jr.), *Pipilo erythrophthalmus aleni*, Jan. 11, and *Corthylio c. calendula*, Jan. 3 (W.P. Wharton) ; Clemson, Oconee Co., on *Hylocichla guttata faxoni*, Nov. 15 (F.C. Bishopp). — TENNESSEE: Nashville, Davidson Co., on *Pipilo e. erythrophthalmus* (Mrs. A.R. Laskey). — UTAH: Hooper, Weber Co. — VERMONT (recorded by Peters, 1936) : Barre, Washington Co., on *Cyanocitta c. cristata*, *Melospiza m. melodia*, and *Junco h. hyemalis* (E.M. Drew) ; Wells River, Orange Co., on *Passerculus sandwichiensis savanna*, Sept. 4 (W.P. Smith). — VIRGINIA: East Falls Church, Arlington Co., on *Cyanocitta c. cristata*, Nov. 26 (E.A. Chapin) ; Annandale, Fairfax Co., 7 flies on heads of young domestic fowl (S.L. Yoder). — WASHINGTON (STATE) : Puyallup, Pierce Co. (C.W. Getzendauer) ; Seattle, King Co., on *Melospiza melodia morphna*, July 31 (Elizabeth Curt) ; Battle Ground, Clark Co., on *Cyanocitta s. stelleri* (J. Beer). — WEST VIRGINIA: Spruce Knob, Randolph Co., on *Junco hyemalis carolinensis* (A. Wetmore). — WISCONSIN (recorded by MacArthur, 1948) : Poynette, Columbia Co., on *Bubo v. virginianus*, Sept. 29 (R. Rausch) ; Cedarburg Swamp, Ozaukee Co., on *Troglodytes aëdon parkmanii* (K.W. MacArthur) ; Tichigan Marsh, Fox River, Racine Co., on *Butorides v. virescens* (K.W. MacArthur) ; Lodi, Columbia Co., on *Bubo v. virginianus* (Frances Hamerstrom) ; Washburn Co., Aug. 10 (R.H. Jones).

MEXICO: Cacahoatán, 600 m., State of Chiapas, on *Busarellus n. nigricollis* (Esc.N.C.Biol.) ; Pano Aguetle, Río Sabinas near Gomez Farias, State of Tamaulipas, on *Glaucidium brasilianum ridgwayi* (G.M. Sutton).

GUATEMALA: Uxactun, Petén, on *Ramphastos s. sulfuratus* (J. Van Tyne).

COSTA RICA: Turrialba, on *Turdus grayi casius* (K.W. Cooper).

PANAMA: (recorded by Ferris, 1930; Dunn, 1934); Chiriqui Province, on *Crypturellus soui panamensis* (L.H. Dunn); Camp Pital, Chiriqui Province, on *Ramphastos swainsonii* (L.H. Dunn).

ANTILLES. CUBA (recorded by Bau, 1922; Aldrich, 1923): without precise locality (E. Poey and J. Gundlach); Santiago de Cuba. — JAMAICA (recorded by Walker, 1849; Austen, 1903; Thompson, 1949): without more precise locality, on *Pseudoscops grammicus* (Walker's ♂ type and another ♂) and *Amazona l. leucocephala* (P.H. Gosse.—Brit. Mus.); Corn Puss Gap, 2000 ft., St. Thomas, on *Amazona collaris* (G.B. Thompson).

COLOMBIA: Piedecuesta, Depto. Santander Sur, on *Otus a. albugularis* (M.A. Carriker, Jr.); Cincinnati, Sa. Marta, Depto. Magdalena, on *Oreopeleia linearis infusca* (M.A. Carriker, Jr.); Chinchicuá, Sa. Marta, Dept. Magdalena, on *Thripadectes f. flammulatus* (M.A. Carriker, Jr.).

VENEZUELA: Colonia Tovar, State of Aragua, on *Otus* sp. [*Scops* sp.] (P. Anduze).

BRAZIL: (recorded by Speiser, 1902; Lutz, Neiva and da Costa Lima, 1915): Humboldt, State of Santa Catharina, on *Ramphastos dicolorus* (W. Ehrhardt); Nova Teutonia, Itá, State of Santa Catharina, on *Buteo magnirostris magniplumis*, *Ramphastos dicolorus*, *Uroleuca cristatella* (3 flies, each with a Mallophagan attached), *Micrastur ruficollis*, and *Pyroderus s. scutatus* (with a Mallophagan attached) (F. Plaumann); Cara Pintada, State of Paraná, on *Micrastur ruficollis*; Eugene Lefèvre, State of São Paulo (J. Travassos); Apuaçu, State of São Paulo, on *Syndactyla r. rufosuperciliata* (G.M. Allen); Mogi das Cruzes, State of São Paulo; City of São Paulo, on *Piaya cayana macroura*; Ilha do Cardoso, State of São Paulo, on *Cyanocorax coeruleus*; Juquía, State of São Paulo, on *Buteo magnirostris magniplumis*, *Cyanocorax caeruleus*, and *Ramphocelus bresilius dorsalis*; Ubatuba, State of São Paulo, on *Tyrannus m. melancholicus*; Boraceia, State of São Paulo, on *Strix hylophila*; Iporanga, State of São Paulo, on *Drymophila ferruginea*; Varjão de Guaratuba, State of São Paulo, on *Hypomorphnus u. urubitinga*; Cantareira, State of São Paulo, on *Ciccaba virgata borelliana* (most of the São Paulo specimens received from the Departamento de Zoologia, São Paulo, through Dr. L. R. Guimarães).

PARAGUAY: Paso Yobai, on *Ramphastos t. toco* and *Colaptes campestris campestroides* (F. Schade).

ECUADOR: Abitagua, 1100 m., Río Pastaza, Prov. Oriente, 2 flies on a thrush, each bearing a Mallophagan (W. Clarke-Macintyre).

ENTOMOLOGICA AMERICANA

PERU: Lima-Chorillos, on *Pyrocephalus rubinus obscurus* (W. Weyrauch); Hacienda Cadena, Marcapata, Cuzco, 100 m., on *Cephalopterus o. ornatus* (C. Kalinowski); Lima, on a fringillid (W. Weyrauch).

BOLIVIA: Incachaca, 2500 m. (J. Steinbach).

CHILE (recorded by E. P. Reed, 1932; Stuardo, 1946): Concon, Valparaiso (A. Wetmore); Puerto Montt, 41° 30' S. (A. Twoney); Valparaiso, on "zorzal," *Turdus magellanicus* (E.P. Reed); Maquehue, Temuco, on "concón," *Strix r. rufipes*, May 15.

There is a possibility that *O. vicina* may be identical with the Old World *O. turdi* (Latreille), in which case the species would be nearly cosmopolitan. Provisionally the two are here regarded as distinct.

As *O. vicina* is often overlooked, owing to its small size, its distribution is incompletely known, even in North America, in spite of the long list of localities and hosts. There are no records from Alaska, Alberta, Manitoba, Saskatchewan, New Brunswick, Nova Scotia, Rhode Island, Delaware, Georgia, Florida, Alabama, Mississippi, Arkansas, Texas, Oklahoma, Michigan, Indiana, North Dakota, South Dakota, Minnesota, Iowa, Nebraska, Montana, Wyoming, Nevada, and Idaho; although it will no doubt be found in several of these areas. The records are sporadic for the Antilles and tropical continental America, where it is nevertheless one of the most common hippoboscids. The northmost locality known is Campbell River, Vancouver I. (50° N.), and the southmost, Puerto Montt, Chile (41° 30' S.). It has not been taken as far north as *Ornithomyia fringillina* and is also much scarcer than the latter in eastern Canada, perhaps because it is less adaptable than *O. fringillina* to short summers and severe winters (Part I, p. 122). Moreover, *O. fringillina*, the most common Nearctic bird-fly, is practically absent from the Neotropics, where *O. vicina* replaces it on passerines and certain other birds.

If *O. vicina* is regarded as specifically distinct from *O. turdi*, it is known outside the New World only from the Hawaiian Islands, where it seems to be a recent introduction by Man. Three flies and one puparium were found by E. H. Bryan in 1921 on a pheasant at Koloa, Kauai. Another specimen was taken recently in Honolulu on a domestic pigeon (Alicata, 1948). Further evidence will have to decide whether the fly is permanently established in these islands.

Known Nearctic Hosts of *O. vicina* (verified individual records in parentheses). Ciconiiformes (2): *Butorides v. virescens* (2). Falconiformes (7 and 1 undetermined hawk): *Accipiter cooperii*

(1); *A. "fuscus"* (1); *Buteo jamaicensis borealis* (2); *B. jamaicensis calurus* (1); *Buteo p. platypterus* (1); *Falco s. sparverius* (1). Galliformes (5): *Bonasa umbellus togata* (1); *Dendragapus obscurus fuliginosus* (1); **Gallus gallus bankiva* (1); *Lophortyx g. gambelii* (2). Strigiformes (33 and 1 undetermined owl): *Aegolius a. acadicus* (4); *Asio f. flammeus* (3); *A. wilsonianus* (3); *Bubo v. virginianus* (11); *B. virginianus pacificus* (1); *B. virginianus pallescens* (1); *B. virginianus saturatus* (1); *Otus a. asio* (1); *O. asio bendirei* (1); *O. asio kennicottii* (1); *O. asio naevius* (1); *Strix v. varia* (1); *S. o. occidentalis* (2); *S. occidentalis lucida* (1); *Tyto alba pratincola* (1). Piciformes (2): *Dendrocopos p. pubescens* (1); *D. pubescens medianus* (1). Passeriformes (153): *Agelaius p. phoeniceus* (2); *Ammodramus savannarum australis*; *Aphelocoma c. californica* (2); *A. californica woodhousei* (2); *Baeolophus bicolor* (1); *Carpodacus mexicanus frontalis* (1); *C. p. purpureus* (1); *Chamaea fasciata phaea* (2); *Cinclus mexicanus unicolor* (1); *Corthylio c. calendula* (2); *C. calendula cineraceus* (2); *Corvus b. brachyrhynchos* (1); *Cyanocitta c. cristata* (6); *C. s. stelleri* (4); *C. stelleri frontalis* (1); *Dendroica a. aestiva* (1); *D. coronata* (1); *D. p. pinus*; *Dumetella carolinensis* (1); *Euphagus cyanocephalus* (1); *Geothlypis trichas brachidactyla* (1); *Hedymeles ludovicianus* (2); *Hylocichla f. fuscescens* (2); *H. guttata fazoni* (2); *H. mustelina* (1); *H. u. ustulata* (1); *Icterus galbula* (2); *Junco* sp. (1); *J. h. hyemalis* (4); *J. hyemalis carolinensis* (1); *J. o. oreganus* (1); *J. oreganus thurberi* (2); *J. phaeonotus dorsalis* (2); *Melospiza* sp. (1); *M. g. georgiana*; *M. l. lincolni* (3); *M. m. melodia* (18); *M. melodia cooperi* (2); *M. melodia gouldii* (1); *M. melodia morphna* (2); *Mimus polyglottos leucopterus* (1); *Mniotilta varia* (1); *Molothrus a. ater* (4); *M. ater obscurus* (1); **Passer d. domesticus* (5); *Passerculus sandwichensis savanna* (1); *Passerella iliaca* subsp. (2); *Penthestes a. atricapillus* (1); *Perisoreus c. canadensis* (1); *Pica pica hudsonia* (1); *Pipilo e. erythrophthalmus* (4); *P. erythrophthalmus alleni* (1); *P. erythrophthalmus canaster*; *P. fuscus carolae* (1); *P. fuscus crissalis* (1); *P. fuscus mesoleucus* (1); *P. fuscus senicula* (1); *P. maculatus falcifer* (1); *P. maculatus megalonyx* (1); *P. maculatus montanus* (2); *Piranga erythromelas* (1); *P. flava hepatica* (1); *Poocetes g. gramineus* (1); *Quiscalus g. quiscula* (1); *Q. quiscula aeneus* (3); *Regulus s. satrapa* (2); *R. satrapa olivaceus* (1); *Richmondia c. cardinalis* (1); *Seiurus a. auricapillus* (1); *S. n. noveboracensis* (1); *Sitta c. carolinensis* (1); *Spizella p. pusilla* (1); *S. p. passerina* (7); *Toxostoma r.*

rufum (1); *Troglodytes a. aëdon* (1); *T. aëdon parkmanii* (2); *Turdus m. migratorius* (6); *T. migratorius propinquus* (2); *Tyrannus tyrannus*; *Wilsonia citrina*; *Zonotrichia albicollis* (3); *Z. coronata* (3); *Z. leucophrys nuttalli* (1).

Known Neotropical Hosts of *O. vicina*. Tinamiformes (1): *Crypturellus soui panamensis* (1). Falconiformes (6): *Busarellus n. nigricollis* (1); *Buteo magnirostris magniplumis* (2); *Hypomorphnus u. urubitinga* (1); *Micrastur ruficollis* (2). Columbigiformes (1): *Oreopeleia linearis infusca* (1). Psittaciformes (2): *Amazona collaris* (1); *A. l. leucocephala* (1). Cuculiformes (1): *Piaya cayana macroura* (1). Strigiformes (7): *Ciccaba virgata borelliana* (1); *Glaucidium brasilianum ridgwayi* (1); *Otus* sp. (1); *O. a. albogularis* (1); *Pseudoscops grammicus* (1); *Strix hylophila* (1); *S. r. rufipes* (1); *Tyto alba furcata*. Piciformes (6): *Colaptes campestris campestroides* (1); *Ramphastos dicolorus* (2); *R. s. sulfuratus* (1); *R. swainsonii* (1); *R. t. toco* (1); *R. vitellinus ariel*. Passeriformes (13 and 2 undetermined passerines): *Cephalopterus o. ornatus* (1); *Cyanocorax caeruleus* (2); *C. c. chrysops*; *Drymophila ferruginea* (1); *Pitangus sulphuratus maximiliani*; *Pyrocephalus rubinus obscurus* (1); *Pyroderus s. scutatus* (1); *Ramphocelus bresilius dorsalis* (1); *Syndactyla r. rufosuperciliata* (1); *Thripadectes f. flammulatus* (1); *Troglodytes m. musculus*; *Turdus grayi casius* (1); *T. magellanicus* (1); *Tyrannus m. melancholicus* (1); *Uroleuca cristatella* (1).

Bionomics. The seasonal fluctuations and host relations of *O. vicina* were discussed in part I (pp. 236–237 and 329–330). I pointed out that it agrees with *Ornithomyia fringillina* in being one of the least specific flies. The host list now comprises 113 native species (153 subspecies), 77 in the Nearctic and 36 in the Neotropical fauna. The list will be greatly extended when the ectoparasites of tropical birds are studied in earnest; but the main features of host choice will probably remain the same.

With regard to interspecific competition (Part I, p. 223), in the Nearctic Region *O. vicina* and *Ornithomyia fringillina* often infest the same species and at times even the same individual bird. Of the 77 native host species of *vicina* and 106 of *fringillina*, 59 have yielded both flies, 51 of these birds being Passeriformes. The few occurrences on the same species of Falconiformes (2), Galliformes (2), Strigiformes (3) and Piciformes (1) are obviously fortuitous, as common bird-flies will unavoidably stray from time to time to common birds. Both *vicina* and *fringillina* evidently favor some of the same passerine birds for breeding, as shown by an analysis

of the verified individual records. Of 198 native Nearctic records for *vicina*, 148 or 75 per cent are from Passeriformes, the corresponding numbers for *fringillina* being 358 and 289 or 80 per cent. These flies differ, however, decidedly in their relations to other types of hosts: *vicina* breeds also regularly on owls (Strigiformes) (34 Nearctic records, or 16 per cent), on which it is sometimes very abundant, whereas *fringillina* strays only occasionally to such birds (8 Nearctic records, or 2.1 per cent). On the other hand, *fringillina* breeds also on Galliformes (25 Nearctic records, or 7 per cent) and Piciformes (18 Nearctic records, or 5 per cent), and more doubtfully on Falconiformes (14 Nearctic records, or 4 per cent), orders on which *vicina* occurs only accidentally (4 Nearctic records, or 2 per cent, on Galliformes; 2, or 1 per cent, on Piciformes; and 8, or 4 per cent, on Falconiformes).

The data are as yet too fragmentary for a more detailed analysis and particularly to decide whether any of the 60 Nearctic passerines are either preferred or only stray hosts. At present, the song sparrow, *Melospiza melodia*, heads the list with 23 verified records, followed by the American robin, *Turdus migratorius*, with 8, and the chipping sparrow, *Spizella passerina*, with 7. These three birds are also favored by *Ornithomyia fringillina*. The remaining passerines are divided as follows: 1 with 6 records, 4 with 5 each, 5 with 4, 6 with 3, 7 with 2, and 28 with 1. The scarcity of records from redwing, *Agelaius phoeniceus*, catbird, *Dumetella carolinensis*, brown thrasher, *Toxostoma rufum*, and cowbird, *Molothrus ater*, is remarkable in view of the decided predilection of *Ornithomyia fringillina* for these birds.

As noted in Part I (p. 229), infestations of Passeriformes with *O. vicina* are usually light, perhaps because they are kept in check by the host (Part I, p. 130). An additional heavy infestation is that of a juvenile *Junco phaeonotus dorsalis*, in Arizona, which carried 14 flies. The species is often abundant on owls, which may be important winter hosts of *O. vicina*, as some owls are permanent, year-round residents in the northern United States. It is as yet unclear how the *O. vicina* of the passerines hibernate. Presumably some adult flies travel south in the fall on the migrating hosts; but whether any return north in the spring is unknown.

The 39 verified Neotropical records are too few to warrant much discussion. The Passeriformes predominate (15, or 38 per cent of the records) and appear to be the main breeding hosts in the tropics. That captures on toucans (Ramphastidae) and tropical owls are few may be due to the fact that small flies are easily overlooked on

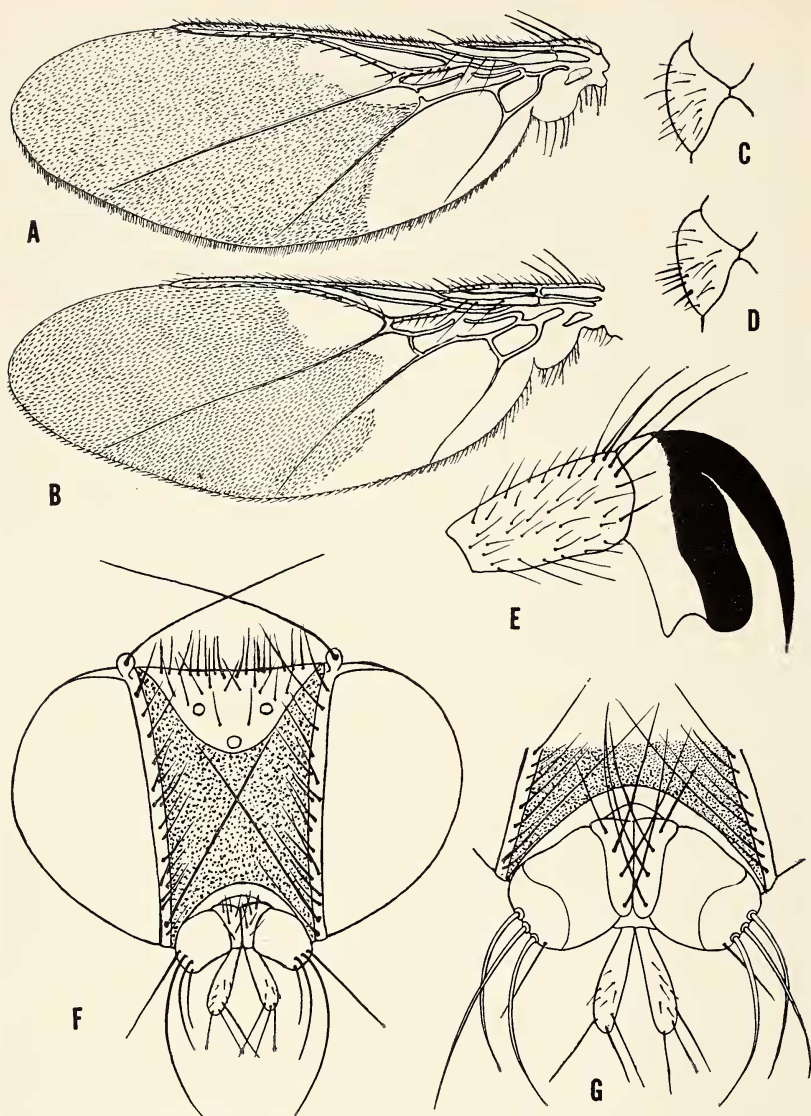


Fig. 24. *Ornithoica vicina* (Walker). A-B, wings showing variation in extent of microtrichia: A, ♀, Ponchatoula, on *Dendrocopos p. pubescens*; B, ♀, Wenham, on *Bubo v. virginianus*. C-D, trochanters of hind legs: C, ♀, Sauvies I., on *Bubo virginianus saturatus*; D, ♂, Nova Teutonia, on *Uroleuca cristatella*. E, distitarsus and claw of hind leg, ♀, Palo Alto, on *Zonotrichia coronata*. F, head, ♀, Orient, on *Pipilo e. erythrophthalmus*. G, frontal area and antennae, ♀ (corrected Fig. 5C).

such birds. Presumably both groups contain true breeding hosts also.

O. vicina is often infested with mites and I recorded 10 cases of phoresy of Mallophaga by this fly (Part I, pp. 151-152 and 167-168).

The puparium (Figs. 23*F-G*) is broadly elliptical from above, scarcely wider posteriorly, lenticular and equally convex on both faces in side view, the edges forming rounded keels. The largest of 3 puparia from the ears of *Bubo virginianus*, at Wenham, is 2.3 mm. long, 2 mm. wide, and about 1 mm. thick. The slightly raised posterior cap is divided dorsally and ventrally by a median depression ending in a curved notch; a deep, circular, apical pit occupies the space between the dorsal and ventral notches. Each half cap, or peripneustic lobe, comprises 3 low, radiating ridges, bearing each 15 to 20 scattered, minute spiracular pores, and separated by shallow and narrow grooves. The integument is bare, shiny and very smooth, with only faint traces of anastomosing engraved lines in a few spots. There is no trace of segmentation; but slight longitudinal depressions set off the lateral keels dorsally and ventrally. Puparia of *O. vicina* are sometimes found in the plumage or ears of owls (Part I, p. 189).²⁸

Affinities. The description of *O. promiscua* by Ferris and Cole (1922), the additional notes by Ferris (1929), and the characters of my key should suffice to recognize *O. vicina*. The wing is 2.8 to 3.7 mm. long. The venational peculiarities are perhaps more reliable for this fly than usual in the family. The apical, deflected part of the 3rd longitudinal vein is usually slightly longer than the basal, free part; it runs almost in contact with the costa or is only narrowly separated; the anal cell is about twice as long as wide or slightly longer; the posterior basal cross-vein ends somewhat before mid-length of the 2nd basal cell. The scutellum bears normally 4 long preapical bristles, in 2 pairs, exceptionally 5 or even 6. There are 15 to 18 inner orbital bristles, a few very long and some very short. The characteristic extent of the microtrichia on the wing, first figured by Lutz, Neiva and da Costa Lima (1915, as *O. confluenta*), varies (Figs. 22 and 24*A-B*), but never approaches that of the true *O. confluenta*. Abnormal additional veins, very unusual in hippoboscids, are shown in Figs. 23*C-E*.

²⁸ Puparia of *Ornithoica pusilla* have recently been reported from the ears of *Asio flammeus sandwichensis*, in Hawaii (Adachi, 1954).

Ferris and Cole (1922) noted that the American *O. vicina* (their *O. promiscua*) and the Old World *O. turdi* (Latreille, 1812) were closely related, the extent of the microtrichia in the wing being about the same in both. Upon comparison, *O. turdi* is somewhat smaller, the wing being only 2 to 2.5 mm. long, with a shorter and wider anal cell, usually about $1\frac{1}{2}$ times as long as its greatest width (in *O. vicina* about twice as long as wide). Since these differences appear to be constant, it is advisable to retain the two species as distinct until the genus is revised on a world-wide basis.

Original description of *O. vicina*: "Picea, capite, humeris, abdominis basi et segmentorum marginibus posticis apice fulvis, femoribus basi coxisque pallidioribus, tarsis piceis, alis subfuscis. Body pitchy, smooth, shining: head, shoulders and base of the abdomen dark tawny: tip of the abdomen beset with black bristles; hind borders of its latter segments pale: legs tawny, clothed with black hairs; thighs at the base and hips pale tawny; feet pitchy; claws black: wings pale brown; veins pitchy; fore border veins at intervals, and wing-ribs pale tawny; second longitudinal vein united to the costal vein long before the end of the latter. Length of the body 1 line [2.2 mm.]; of the wings 4 lines [span of wings, 8.8 mm.]." Dr. F. van Emden, who examined the type at the British Museum at my request, sent me the following information, which I confirmed later (1951) myself. The type is a male, the protruding penis ending in a broadish lamina of chitin. Microtrichia cover slightly more than the apical half of the wing, forming only a small patch at the apex of the 3rd posterior cell. The interocular face is slightly wider than an eye, hardly widened at postvertex, almost parallel-sided. The wing is 3.7 mm. long. These characters are those of the common American species. Although Walker mentioned only one specimen, a second male, from the same host, "*Ephialtes* [*Pseudoscops*] *grammicus*," and locality, now stands with it. This has a slightly wider interocular face than the type, but agrees otherwise.

Original description of *O. promiscua*: "Female. Length (on slide) 2.5 mm. A yellowish-brown species, the thorax darker than the legs. Head with the frons [interocular face] probably almost parallel-sided in perfect specimens but in the holotype curving in slightly. Frontal orbits with at least three strong setae and several smaller setae. Ocellar setae small. Ventral side with a row of slender setae more or less paralleling the orbits. Thorax with several short, stout, black setae on the humeral callosities and on the margin in front of the wing. Mesonotum with numerous small, pale setae, all with distinct pustulations about the base. There is a single long seta just behind the humeral callosity, two in front of the wing and one just behind the wing. Scutellum with small, pale, pustulated setae on the disc and with four long, black setae. Halteres rather small and delicate. On the ventral side both meso- and meta-sternum are beset with numerous fine setae, mingled with a few that are small and stout. Wings with a well-defined anal cell; R_{2+3} [3rd longitudinal] distinctly curved toward the costa and bristly to the tip; *m-cu* [anterior basal] cross-vein broken, the upper part obsolete; vein above cell 2M [4th longitudinal], broken near the middle; distal half of the wing covered with microscopic setulae as shown in the figure. Legs comparatively strong, the anterior femora noticeably thickened; setae arranged in a rather definite fashion, as shown in the figure. Claws rather slender. Abdomen above with a chitinated basal plate extending from side to side, with four quite large plates occupying the median half and with a small plate on each side of the anal region, the basal plate and the succeeding four with numerous small setae and the para-anal plates or their immediate region with two long setae. Lateral margins with a number of small, stout

setae which are borne on tubercles. On the ventral side there is a median region beset with small setae, a region along the anterior, lateral margin with numerous setae on tubercles and a smaller region of these near the genital opening. Near the genital opening there is also a pair of small plates bearing several slender setae." I have seen the original type series of *O. promiscua*, all females mounted on slides, the holotype and one paratype, at the California Academy of Sciences, and two paratypes, at Stanford University; also the two flies, both females, tentatively referred to *promiscua* by Ferris and Cole. All these specimens belong to what is here called *O. vicina* (Walker).

Original description of *O. melaleuca* (translated from the German): "Larger species. Abdomen white, metallic greenish-black above, with white margins of the segments. Head mahogany-brown above, yellowish-brown on vertex, also lighter on the side margins, without sharply defined darker spot in the middle. Antennal appendages shiny blackish-brown, with the 3 setae curved downward, as drawn by Rondani. Eyes pale brownish-red (specimen preserved in spirit, hence the color may be somewhat faded). Ocelli black. Head tawny-yellow beneath. Mesonotum depressed medially before the scutellum, metallic blackish-green. Humeral callosities pale yellowish-brown as in the other species, covered with scattered black hairs; a broad pale yellowish-brown streak runs from the humeral callosities to below the bases of the wings. Scutellum with black setae at the margin. Upper femora of fore legs not especially thickened, pale yellowish-brown with a broad brown longitudinal streak above, which covers them almost completely except at the base. Upper femora of mid and hind legs almost entirely pale brown, except for the broad pale yellow base. Fore tibiae brown with paler base. Mid and hind tibiae pale brown, with the narrow yellow ring at the basal third present also in some other species. Tarsi brown, the first segments with pale rings. Claws black. Wings lightly clouded with gray; the venation exactly as figured by Speiser, therefore not as shown by Rondani, whose figure is erroneous (according to Speiser's and my observation). Halteres yellowish gray-white. Abdomen almost pure white, with a weak yellowish-gray tinge, sparsely black hairy above and below; the first 5 segments (here distinct, as contrasted with most other hippoboscids) above with very broad, shiny greenish-black bands, which leave free only the white margins and sides of the segments. The first black band continues on each side into a short, likewise black pleurite. Last segment grayish-white, with a shiny black streak at the side margins, beneath with numerous punctiform warts and with black setae. Length in spirit 3.1 mm.; from oral margin to hind margin of scutellum, 1.9 mm.; of wing, 3.5 mm." I have not seen the type, which should be at the Berlin Museum. *O. melaleuca* is here referred to *O. vicina* from the description and Bau's key. These mention no truly specific character, color differences being wholly unreliable in this genus. I have seen Cuban specimens differing in no respect from other *O. vicina*.

Ornithoica confluenta (Say)

Figs. 25A-C and 26A-B

Ornithomyia confluenta Say, 1823, Jl. Ac. Nat. Sci. Philadelphia, 3, p. 103 (no sex. United States, without more precise locality, on "*Ardea candidissima*" [*Leucophoyx t. thula*]. Type lost); 1837, Oeuvres Entomologiques, edit. by Gory, p. 104; 1859, Complete Writings, edit. by Leconte, 2, p. 88.

Ornithoica confluenta Speiser, 1900, Ann. Mus. Civ. Stor. Nat. Genova, 40, p. 558 (no specimen seen); 1907, Ent. News, 18, p. 103 (in part). Bau, 1922, Centralbl. Bakt. Parasit., Abt. 2, 57, p. 278; 1929, Zentralbl. Bakt. Parasit., Abt. 2, 79, pp. 247 and 248 (in part). J. Bequaert, 1940, Mem. Soc. Cubana Hist. Nat., 14, p. 326. MacArthur, 1948, Bull. Publ. Mus. Milwaukee, 8, No. 4, p. 394. Not of most authors.

- Anthoica* (?) *confluente* Coquillett, 1899, *Canad. Entom.*, **31**, p. 335.
- Ornithoeca confluenta* Speiser, 1908, *Zeitschr. Wiss. Insektenbiol.*, **4**, p. 303 (in part).
- Ornithomyia confluens* Wiedemann, 1830, *Aussereurop. Zweifl. Ins.*, **2**, p. 611 (emendation of *confluente*; specimen possibly seen, although Say's description is copied; locality surmised to be Pennsylvania). Osten Sacken, 1858, *Cat. Dipt. North America*, p. 86; 1878, *Smithson. Misc. Coll.*, No. 270, p. 214. Bigot, 1885, *Ann. Soc. Ent. France*, (6), **5**, p. 229.
- Ornithoica confluens* Aldrich, 1905, *Smithson. Misc. Coll.*, **46**, No. 1444, p. 655 (in part).
- Ornithoica confluenta* var. *exilis* Bau, 1929, *Zentralbl. Bakt. Parasit., Abt. 2*, **79**, pp. 247 and 248 (in part: record from Amboina, on "*Ardea alba*" only). Not *Ornithomyia exilis* Walker, 1861.
- Ornithoica beccariina* Rondani, 1878, *Ann. Mus. Civ. Stor. Nat. Genova*, **12**, p. 160, fig. (no sex. Amboina: on "*Ardea alba*" [*Casmerodius albus modestus*]). Two ♀ cotypes on one pin and one ♀ cotype mounted on a slide by Ferris, all at Genoa Mus.). v. Röder, 1892, *Jahrb. Hamburg. Wiss. Anst.*, **10**, pt. 2, p. 206. Speiser, 1900, *Ann. Mus. Civ. Stor. Nat. Genova*, **40**, pp. 557-559, fig. (in part: 3 cotypes only; new description, but sex not determined). Bau, 1922, *Zentralbl. Bakt. Parasit., Abt. 2*, **57**, p. 278. Ferris, 1929, *Canad. Entom.*, **61**, p. 281, figs. 1 and 2A (♀ cotype of Rondani, with descriptive notes).
- Ornithoica podicipis* v. Röder, 1892, *Jahrb. Hamburg. Wiss. Anst.*, **10**, pt. 2, p. 206 (no sex. Zanzibar: on *Podiceps* sp. Cotypes at Hamburg Mus., now destroyed, and in the v. Röder Coll., now at the Zoolog. Institut, Halle a. S.). Speiser, 1900, *Ann. Mus. Civ. Stor. Nat. Genova*, **40**, p. 559. Bau, 1922, *Zentralbl. Bakt. Parasit., Abt. 2*, **57**, p. 278. Ferris, 1929, *Canad. Entom.*, **61**, p. 285 (locality given by error as Australia).
- Ornithoeca podicipis* Speiser, 1907, *Wiss. Ergebn. Schwed. Zool. Exped. Kili-mandjaro Meru*, **2**, pt. 10, p. 3; 1908, *Zeitschr. Wiss. Insektenbiol.*, **4**, p. 245. Bezzi, 1908, *Bull. Soc. Ent. Italiana*, **39**, (for 1907), p. 197. Neave, 1912, *Bull. Ent. Res.*, **3**, p. 318. Aders, 1917, *Op. cit.*, **7**, pt. 4, p. 400 (Zanzibar: on a species of heron).
- Ornithoica confluenta* var. *podicipis* Bau, 1929, *Zool. Anzeiger*, **85**, p. 11 (saw 5 cotypes from Hamburg Mus., now destroyed, and 4 cotypes in the v. Röder Coll. at Zoolog. Institut, Halle a. S.; new description, but sex not determined); 1929, *Zentralbl. Bakt. Parasit., Abt. 2*, **79**, pp. 247 and 248 (notes on cotypes).

Distribution and Specimens Examined. UNITED STATES.

FLORIDA: two ♀ without more definite locality, on *Casmerodius albus egretta*, at M.C.Z. (J.A. Allen, 1863). Say's original specimen or specimens may also have come from Florida.

ANTILLES. BAHAMAS: Booby Cay, Mariguana Island, 19 ♀ on *Butorides virescens bahamensis*, July 21, 1930 (H.S. Peters).

VENEZUELA: Cantaura, State of Anzoategui, 6 ♀ 2 ♂ on *Bubulcus i. ibis*, Aug. 25, 1948 (F.D. Smith).

BRAZIL (specimens received from the Departamento de Zoologia, São Paulo, through Dr. L.R. Guimarães): State of São Paulo, without more precise locality, 1 ♀ on *Casmerodius albus egretta*, June, 1946; Osasco, State of São Paulo, 5 ♀, 1 ♂ on *Casmerodius albus egretta*, July 26, 1946.

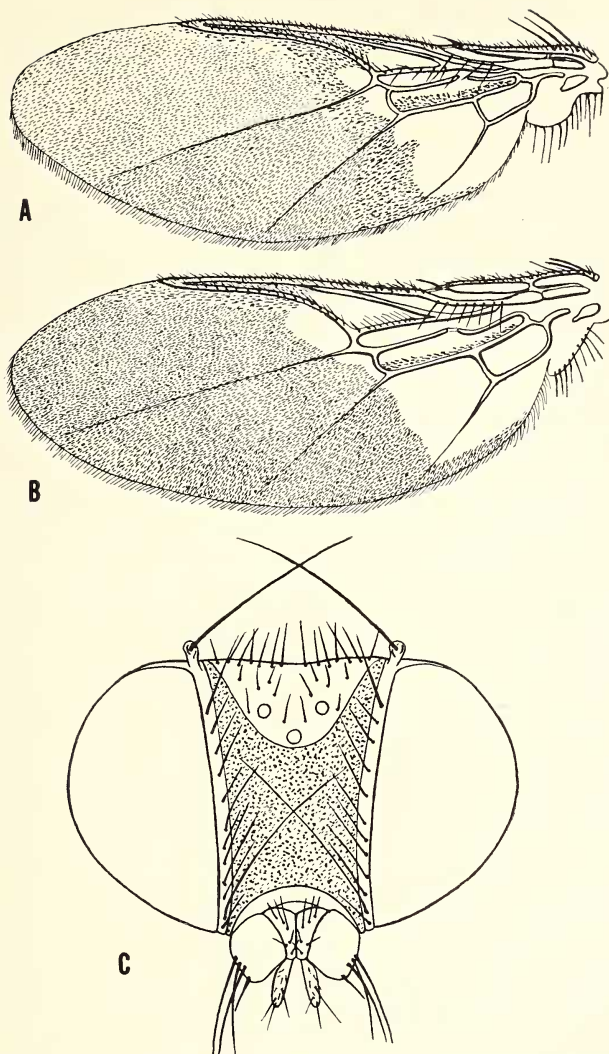


Fig. 25. *Ornithoica confluenta* (Say). A-B, wings: A, ♀, Booby Cay, on *Butorides virescens bahamensis*; B, ♀ cotype of *Ornithoica beccariina* Rondani, Amboina, on *Casmerodius albus modestus*. C, head, ♀, same data as A.

If the synonymy here proposed is correct, *O. confluenta* will be world-wide, at least in tropical and subtropical areas. In the Old World there are reliable published records from Zanzibar I. and Indonesia (Amboina). I have also seen specimens from Africa (Daressalaam, Tanganyika Terr., on egret; Zanzibar I., on small buff-backed heron; Butiaba, Uganda, on *Ixobrychus minutus payesi*; Leopoldville, Belgian Congo, on heron; Old Blantyre, Nyasaland, on small heron) and Madagascar (on *Bubulcus ibis*).

The following published records for *O. beccariina* do not refer to the true *O. beccariina* (= *confluenta* Say), from wading birds, but to *Ornithoica pusilla* (Schiner): Speiser, 1900, Ann. Mus. Civ. Stor. Nat. Genova, **40**, p. 557 (specimen from Stephansort, New Guinea, on *Diphyllodes magnificus*, a bird of paradise); Speiser, 1902, Termész. Füzetek, **25**, p. 334 (New Guinea: near Simbang on Huon Gulf, without host; Friedrichs-Wilhelmshafen, on *Dacelo* ["*Sauromarptis*"] *gaudichaud*, a kingfisher); Ferris, 1924, Ent. News, **35**, p. 235 (Borneo; referred to *pusilla* by Ferris, 1929). I have seen specimens of *O. pusilla* from *Dacelo gaudichaud*, from Hollandia, New Guinea (H. Hoogstraal Coll.).

Known American Hosts of *O. confluenta* (verified individual records in parentheses). Ciconiiformes (5): *Casmerodius albus egretta* (3); *Bubulcus i. ibis* (1); *Butorides virescens bahamensis* (1); *Leucophoyx t. thula*.

Bionomics. *O. confluenta* has now been taken in America on six occasions from four different species of waders. It occurs in the Old World also on this type of host and is evidently a specific parasite of Ciconiiformes. I suspect that it is more common than the few recorded captures might indicate. If it actually uses only wading birds as breeding hosts, its small size might make it difficult to find and to collect on large birds with very long plumage. Possibly also it may be restricted to tropical and subtropical areas, where little collecting of ectoparasites has been done. Sometimes it seems to be fairly abundant on an individual host. The single record from a grebe (*Podiceps*) in Africa may have been based either on a stray or on a contamination. The puparium is as yet unknown.

Affinities. Until recent years, Say's trivial name *confluenta* was applied to the common American *Ornithoica* of passerine and other birds, in the belief that the genus contained only one species in the New World. When it was found that American wading birds harbor another species, the question arose as to how Say's name should be used. The type is lost and the original description fits either species. However, Walker's later name *vicina* is certainly

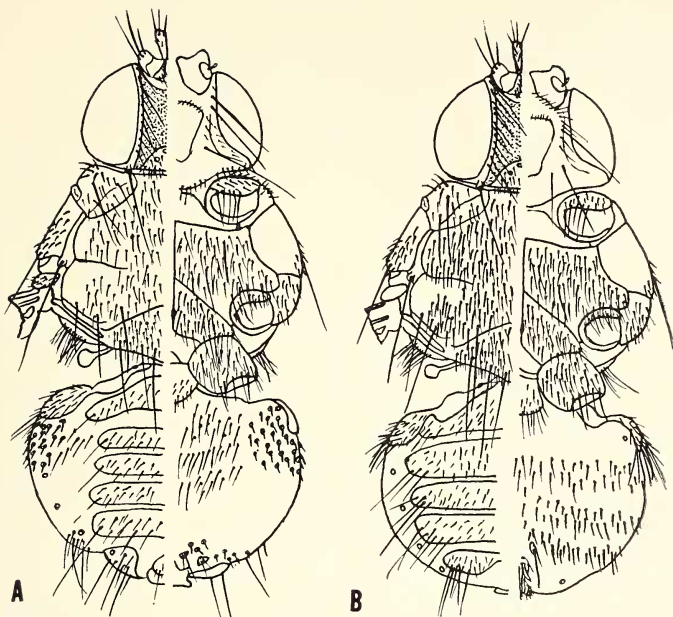


Fig. 26. *Ornithoica confluenta* (Say). Body in dorsal and ventral view: **A**, ♀, Booby Cay, on *Butorides virescens bahamensis*; **B**, ♂, Osaseo, on *Casmerodius albus egretta*.

based upon the common species from non-wading birds, as shown by his type. Since, on the other hand, Say's species was originally described from a wader, it seems reasonable to use his name *confluenta* for the species known at present only from waders. There is nothing in Say's description to contradict this. The only other alternative would be to discard Say's name altogether and call the louse-fly of waders by the next older name, *Ornithoica beccariina* Rondani; but such a course seems both unnecessary and unfair to the Father of American Entomology.

O. confluenta is about the size of *O. vicina*, the wing being 3 to 3.6 mm. long. The apical confluent stretch of the 3rd longitudinal vein is nearly as long as the basal free portion and is separated from the costa by a narrow membrane almost to the very tip. The pilosity of the body is somewhat more developed than in *vicina*: the inner orbit bears a row of 8 to 12 setae and the scutellum 3 or 4 pairs of preapical bristles, some longer than others. I am unable to separate the Old World *O. beccariina* Rondani and *O. podicipis* v. Röder from the American species here called *confluenta*.

Original description of *O. confluenta*: "Reddish-brown; costal nervures of the wing confluent before their termination. Vertex with a deeper brown spot; occiput pale yellowish; humerus with a pale spot, the angles not at all produced, obtuse; costal nervures fuscous; feet yellow-brown, tibia with a dark-brown line, nails black. Length rather more than $\frac{1}{10}$ of an inch [2.5 mm.]. The remarkable character of the costal nervures of this species sufficiently distinguish it from others; these nervures are confluent about half the length from the termination of the first cellule to their tip." Say gave no locality and there is no proof whatsoever that his type came from Pennsylvania, as Wiedemann surmised.²⁹ C. W. Johnson (1922, p. 80) supposed that the type might have been collected either in Pennsylvania or west of the Missouri, rather a wide range of territory. More probably it came from Florida, where the snowy egret, the type host, was very common in Say's time. Although Wiedemann merely copied Say's original description, he may have received a specimen, since he did not precede the name with a cross ($\dagger$), a sign he used for species he did not see. It would be interesting if a Wiedemann specimen could be traced at the Vienna Museum or elsewhere, as it would be the only type extant.

Original description of *O. beccariina*: "Long. corp. mill. 2-2 $\frac{1}{4}$. Nigricans, humeris aliquando sordide testaceis. Antennae apice magis vel minus pallido, setis apicalibus nigris, paucis, longis, una longiore. Alae dilute fuscae, vena costale punctis pallidis notata, aliquibus, prope basim, uno contra apicem venae secundae longitudinalis, quae in costa satis distat a tertia magis quam tertia a quarta: transversa intermedia antice incompleta et magis proxima exteriori quam axillari: istarum exteriore satis ante apicem sita tertiae longitudinalis. Pedes plus vel minus nigricantes, femoribus basi, et annulo medio tibiæ, praesertim posticarum, pallidioribus vel sub-testaceis." Speiser (1900) published some additional information, after examining Rondani's types; but it is not certain that the following remarks (translated from the German) refer all to these types, since he studied also a specimen from a bird of paradise, most probably belonging to *O. pusilla* (Schiner). He states that, in addition to the humeral callosities, the episterna [anepisterna] of the mesothorax also are brownish-yellow and that Rondani's figure of the venation is erroneous: "while a small angle is produced where the cubitalis [3rd longitudinal] branches from the radialis [2nd longitudinal], the knee-like bend of the discoidalis [4th longitudinal] enters this angle, so that the anterior basal cell [1st basal] is actually equally wide throughout in *beccariina* also. . . . The entire surface of the wing is very slightly clouded with gray; the veins are brown, but white at certain characteristic spots, however not discolored but seemingly with white pigment. These spots are: in the costalis [costa] a small stretch beyond the basal cross-vein [humeral cross-vein], as well as at both sides of the tip of the subcostalis [subcosta]; its extremity also is white; furthermore the knee-like upward bend of the discoidalis [4th longitudinal] and the anterior half of the posterior cross-vein." A new, corrected figure of the venation is added. The characteristic pattern of microtrichia, specific for *confluenta*, was first shown by Ferris (1929), drawn from a female cotype of *beccariina*, together with the dorsal and ventral aspects of thorax and abdomen. These figures leave no doubt that the *Ornithoica* usually occurring on waders in the New World, is identical with what Rondani described as *beccariina*. Ferris' remarks on this type follow: "It may be noted especially that in the wing the vestiture of minute setae, which occur on both sides of the wing, extends from the vein M_2 (2nd cross-vein) [posterior cross-vein] across the cell Cu [3rd posterior] into the apex of the second anal cell [axillary]. The abdomen possesses four tergal plates in addition to the basal and the paired

²⁹ Wiedemann (1830, 2, p. v) assumed that all Diptera described without locality, which he received from Say, were collected in Pennsylvania, probably because they were sent from Philadelphia.

sub-apical plates. At the lateral margins, just caudad of the basal plate and extending well around onto the ventral side, is an area beset with strong tubercles, each of which terminates in a small, stout, thorn-like seta. There is also a cluster of such tubercles, in part bearing more than one seta, on each side of the venter near the apex. One of these, on each side bears a cluster of slender setae. On the lateral margin of the dorsum, just cephalad of each sub-apical plate, is a conspicuous cluster of large, slender setae. The legs show no distinctive features. There is no spur at the apex of the posterior tibiae and the trochanters of the posterior legs are devoid of stout black setae." Ferris points out that *O. beccariina* differs from both *O. vicina* (which he calls *confluente*) and *O. pusilla* in the distribution of the microtrichia on the wing, since in both last-named the microtrichia enter the 3rd posterior cell only at its extreme apex and are not present in the axillary cell at all. *O. pusilla* agrees with *beccariina* in having a tuft of long, slender setae on the lateral margin of the abdomen just cephalad of the sub-apical plates, which tuft is entirely lacking in *O. vicina*. I have recently (1951) examined the type series of *beccariina* at the Genoa Museum. It now consists of a pin bearing two dry specimens, apparently both females, and an additional female mounted on a slide (by Prof. Ferris). These types confirm the conclusion reached from published information. Their wings are 4 mm. long.

Original description of *O. podicipis* (German text translated): "Nigra; humeris, lateribus thoracis pedibusque flavis, alis dilute fuscis. Long. corp. 2½ millim., long. alar. 3 millim. The venation is in this species also almost the same as in the other two species [*beccariina* Rondani and *turdi* Latreille]. The 3rd longitudinal unites over its apical third with the costa. The anal cell is very distinct. As for distinguishing the 3 species of *Ornithoica*, the anterior basal cell [1st basal cell] is widened in *beccariina*, but of equal width throughout in *podicipis* and *turdi*. The distinction between *podicipis* and *turdi* is in the longer united stretch of 3rd longitudinal and costa in *podicipis*, while this union is much shorter in *turdi*. The posterior basal cell [2nd basal cell] is somewhat shorter than the anterior [1st] in *podicipis*; both basal cells are of about the same length in *turdi*." Both Speiser and Bau pointed out that the 1st basal cell is of equal width throughout in *beccariina* also (Rondani's original figure being erroneous in this respect). Bau (1929) gave a new detailed description (here translated from the German) of the types of *podicipis*, which he regarded as a variety only of *confluente*: "Vertex [interocular face] flat, parallel-sided, dull grayish-brown, the inner orbits strongly raised and swollen, on the occiput [postvertex] with two long setae and likewise above the antennae with two long setae, curved backward. Antennal appendages with one strong and two smaller setae, curved downward. Maxillary palpi short, straight, extending only a little beyond the antennal appendages. Head at sides and beneath dirty yellow to brownish-yellow, with a few setae beneath. Thorax and scutellum grayish-brown, the weakly produced humeral callosities dirty yellow, but in one specimen scarcely paler. Scutellum posteriorly with a few long, erect setae. Pleura dirty yellow, with a broad, dark brown longitudinal streak above the coxae, the streak sharply defined in two specimens only, blurred and indistinct in the others. Wings with the characteristic venation of *Ornithoica*, brownish smoky-gray, in the basal third with a broad, not sharply defined, whitish, almost vitreous cross-band, which includes the cross-veins. The darker areas of the base and apical half of the wing are due to a microscopic pilosity of the wing surface (according to Ad. Lutz). The veins with the usual interrupted white stretches. The 2nd longitudinal ends far beyond the imaginary extension of the small cross-vein [anterior cross-vein]; the imaginary extension of the anal cross-vein toward the costal margin falls on the whitish pigmented elbow of the 4th longitudinal (as in *beccariina*, according to Speiser). Anterior [1st] basal cell equally wide throughout; posterior [2nd] basal cell shorter than the anterior [1st] for about the length of the small [anterior] cross-vein. Posterior [anterior basal] cross-

vein almost completely white-pigmented, scarcely visible in some specimens. Legs: fore femora yellow to dirty yellow, mid and hind femora yellowish at base only, otherwise more or less brownish; all femora with erect, long setae. Fore and mid tibiae yellowish-brown, more brownish in some specimens, the hind tibiae darker brown with a yellow, usually inconspicuous ring at basal third; first two tarsal segments, particularly of the hind legs, with a basal yellow ring. Some specimens have also a trace of a yellow ring at the basal third of the mid tibiae. Outer surface of tibiae with a few long setae placed far apart. Claws simple, bidentate, black. Abdomen dark brown, paler beneath, setose at apex. Length $2\frac{1}{2}$ mm. Wing 3 mm." I have not seen any of the types of *podicipis*; but the available information is sufficient to regard it as identical with *O. confluenta* of wading birds, rather than with the common African *O. turdi*.

Austen (1903, p. 263) considered that the type of *Ornithomyia exilis* Walker (1861, p. 254; no sex; no host; New Guinea: Dorey) was not separable from *O. beccariina* Rondani; but I do not agree with this conclusion. Dr. F. van Emden, who examined the type of *C. exilis* at my request at the British Museum, kindly sent me a sketch of the extent of the microtrichia on the wing. This is as in *O. vicina*, not as in *O. confluenta* (= *beccariina*). I confirmed this later (1951) by direct examination. The true identity of *Ornithomyia exilis* (Walker) is outside the scope of the present paper.

2. SUBFAMILY ORNITHOMYIINAE

Ornithomyia Latreille, 1802

- Ornithomyia* Latreille, 1802 (An X), Hist. Nat. Crust. Ins., 3, p. 466 (with description; monotypic for *Hippobosca avicularia* Linnaeus, 1758); 1803 (An XI), Nouv. Diet. Hist. Nat., 16, p. 380 (with fuller description; same type).
- Ornithomyia* Latreille, 1804 (An XII), Nouv. Diet. Hist. Nat., 24, Tabl. Méthod., pp. 197 and 198 (author's emendation of *Ornithomyia*; monotypic for *Hippobosca avicularia* Linnaeus, 1758); 1805 (An XIII), Hist. Nat. Crust. Ins., 14, p. 402.
- Ornithomyia* Fabricius, 1805, Syst. Antliat., p. 338 (error for *Ornithomyia*, in the combination *Ornithomyia avicularia* Latreille, as a synonym of *Hippobosca avicularia*).
- Ornithomys* "Latreille" Meigen, 1804, Klassif. Beschreib. Europ. Zweifl. Ins., 1, pt. 1, p. xxiii (error for *Ornithomyia*).
- Ornithomyza* "Leach" Zetterstedt, 1842, Dipt. Scandinaviae, 1, p. 82 (with description, but without species); 1848, *Op. cit.*, 7, p. 2902; 1849, *Op. cit.*, 8, p. 3366 (possibly an emendation of *Ornithomyia*; same type, *Hippobosca avicularia* Linnaeus, the only species mentioned in 1848, by present designation).
- Ornythomia* Lasalle, 1844, Bull. Soc. Hist. Nat. Dépt. Moselle, Metz, 2, p. 20 (error for *Ornithomyia*, in the combination *Ornythomia viridis* "Degeer," on *Hirundo rustica* [= *Ornithomyia biloba* Dufour, 1827]; also spelled *Ornythomyia* on pp. 21 and 22).
- Ornithymia* "Latreille" Bezzi, 1904, Kat. Paläarkt. Dipt., 4, p. 277 (error for *Ornithomyia*).
- Ornithomyia* Shipley, 1911, Science Progress in 20th Century, London, 5, (for 1910-1911), No. 20, p. 570 (error for *Ornithomyia*).
- Ornithomyia* Bezzi, 1892, Bull. Soc. Ent. Italiana, 24, p. 148 (in the combination *Ornithomyia avicularia*; error for *Ornithomyia*). [*Ornithomyia* Dugès, 1887, was used in the combination "*Ornithomyia villadae*" for a species of *Lynchia*.]
- Ornithomia* Kirby and Spence, 1826, Introduction to Entomology, 4, p. 86 (in the combination *Ornithomia avicularia*; error for *Ornithomyia*).

- Ornithomyia* E. P. Reed, 1932, Rev. Chilena Hist. Nat., 35, (for 1931), p. 102 (error for *Ornithomyia*, in the combination *Ornithomyia chiliensis* E. C. Reed = *Ornithomyia parva* Macquart).
- Ornithomayia* Kishida, 1932, in Esaki, Iconogr. Insect. Japon., p. 244 (error for *Ornithomyia*, in the combination *Ornithomayia aobatonis* Matsumura = *Ornithomyia avicularia* Linnaeus).

Generic Characters. Fully-winged parasites of birds, not metallic-greenish, often with dull-green pigment in the haemolymph visible through the integument in life. Head inserted between prominent humeral callosities; occiput covering anterior margin of thorax. Ocelli present in most species, sometimes small; more rarely rudimentary or lacking. Eyes large, occupying most of sides of head, with many minute, well-defined ommatidia. Postvertex and frons far apart; intervening soft mediovertex much longer than either. Occipital margin straight or slightly arched. Frons divided by a deep transverse suture into a broad lunula (usually with a median pit or depression) and a narrow interantennal area; the latter rather long basally, ending in a narrow, evenly concave emargination; apical arms moderately long, diverging, mostly membranous except for narrow sclerotized edges near the antennal pits. Antennae medium-sized: 1st segment at least partly separated by a suture from side of lunula; 2nd segment with a moderately long appendage, slightly widened basally and gradually narrowed to a blunt point, not extending to tips of palpi; both appendages diverging, leaving apical arms of frons and palpi fully exposed; arista flattened, gradually widened, slightly spatulate at apex. Palpi moderately long. Pronotum very short, not visible from above. Humeral callosities large, produced forward as broad, bluntly pointed lobes; posthumeral suture deep at sides, superficial or vestigial medially; prothoracic spiracle very large, placed close to hind margin of callosity. Anterior margin of prescutum nearly straight; transverse mesonotal suture deep, straight, narrowly or broadly interrupted medially, usually placed before hind third of mesonotum; anterior ridge of parascutellum fused with mesoscutum; median notal suture superficial, but complete from anterior margin to near scutellum; notopleuron set off throughout from prescutum, wedge-shaped, very narrow anteriorly, much broader posteriorly. Dorsal portion of anepisternum broad, lathe-shaped, parallel-sided, with blunt, scarcely or not projecting outer hind edge. Scutellum large, elliptical, with strongly convex hind margin; surface flat, with a slight median triangular depression connected with a more or less pronounced preapical transverse groove; scuto-scutellar suture mostly deep, superficial at extreme sides.

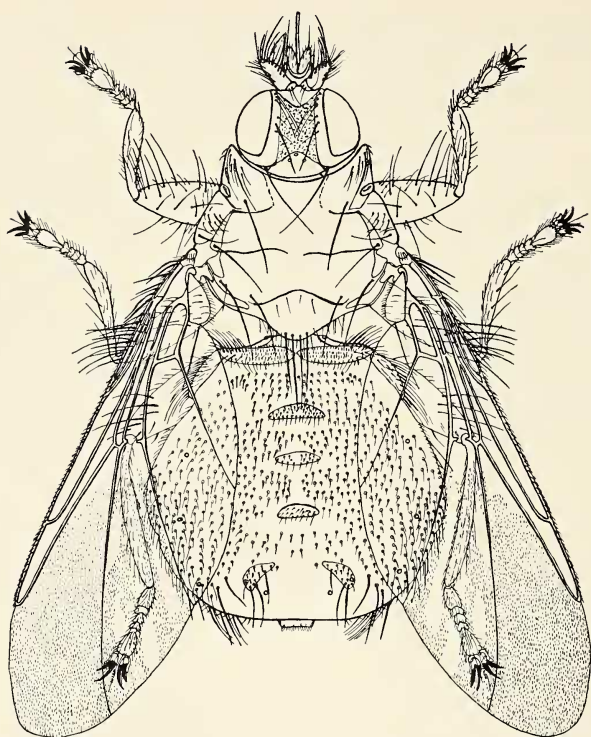


Fig. 27. *Ornithomyia fringillina* Curtis, ♀, Berkeley, on *Passerella iliaca*, subsp. × about 13.

Pleurotergite of metathorax low, transverse, convexly swollen, without process. Basisternum of prothorax separated from mesosternum by a complete suture, forming two broadly triangular, bluntly conical, intercoxal lobes. Mesosternum divided into basisternum and furcasternum by a complete, broadly V-shaped suture (with blunt forward angle ending in a furcal pit). Metasternum undivided, sharply triangular anteriorly, its hind margin slightly produced and evenly rounded in the middle; no metasternal spur near hind coxa. Median longitudinal suture over part or whole of mesosternum only. Metathoracic spiracle placed as in *Ornithoctona*. Legs long, moderately robust; femora slightly swollen; tibiae flattened; tarsal segments 1 to 4 short, broad; hind basitarsus much lengthened, in both sexes with a transverse basal comb of stiff setae beneath (Fig. 29*F*); tips of all tibiae normal; tibial spurs weak.

Claw (Fig. 29E) divided throughout into two teeth of about equal length, the terminal one very sharp, the inner one blunter; in addition, a shorter, tooth-like, but blunt, basal "heel" (claw seemingly tridentate). Wing large, with the complete venation for the family (Fig. 13A), including three cross-veins; anterior basal cross-vein placed almost at, or a short distance basad of, anterior cross-vein; 1st and 2nd basal cells of about equal length; 2nd basal cell at least twice as long as anal cell; 1st, 2nd and 3rd longitudinal veins ending at a sharp angle in the costa; subcosta complete, ending in costa; small bullae in anterior basal cross-vein and in basal elbow of 4th longitudinal; posterior basal cross-vein slanting, upper apical corner of anal cell acute; costa and basicosta setulose; all other veins bare; no strong bristle on costa basad of apex of 1st longitudinal vein; membrane partly covered with microtrichia on upper side; also on under side over a small area at the apex of the 1st posterior cell, which appears darker as a result; alula very large; calypteres much reduced; upper calypter very short, partly thickened at the setulose margin, separated by deep notches from both alula and lower calypter; the latter a narrow, semi-membranous ledge continuous with the posterior ridge of the parascutellum, with thickened, finely setulose hind margin. Abdomen dorsally with a few small, median sclerites, sometimes reduced to the preanal pair; basal pleurotergites fused medially; no striate median area. Seven pairs of abdominal spiracles placed as in Figs. 28 A-B. Body moderately setose; orbital bristles few, in one row; one vertical bristle on each side; under side of head with many bristles on the lateral ridges bordering the buccal cavity; chaetotaxy of thorax mostly obscured; disk of mesonotum nearly bare; sometimes a few distinct prescutellars and a few short postalars; one long notopleural; scutellum with an apical fringe of soft hairs and a row of preapical bristles, the disk with or without short setae; pleurotergite setulose. Abdomen fairly uniformly covered with short setae; longer bristles in certain areas or on the tergal sclerites. Male terminalia (Figs. 29C-D) as in *Ornithoctona*: gonocoxites reduced to very small, finger-shaped, setigerous lobes (easily overlooked); two penis valves slender, sharply pointed; penis also slender, rod-like, bluntly pointed.

Ornithomyia is cosmopolitan, but perhaps more common in temperate than in tropical areas. It occurs on a variety of birds; some species have a wide range of hosts belonging to unrelated orders; the more specialized forms are restricted to the Hirundinidae. Many species have been described, but probably not more than 10 or 12 are valid. *Pseudornithomyia*, originally based on a species

without ocelli, is here treated as a subgenus only of *Ornithomyia*. The development of the ocelli varies greatly in this genus, sometimes even within specific limits (*O. inocellata* Ferris). The reduction or loss of ocelli is not correlated with any other peculiarity of structure. Of the 4 American species, 3 are precinctive, the fourth, *O. fringillina*, being Holarctic and extending farther north than any other hippoboscid (Part I, pp. 121-122 and the discussion of geographical distribution in Part II).

Key to Palearctic and American Species of *Ornithomyia*

1. Ocelli rudimentary or absent. Upper orbit (measured behind the middle of the eye) at least as long as width of inner orbit. Prosternal lobes sharply triangular, about as long as wide at base. Nearly apical two-thirds of wing membrane covered with microtrichia. Wing 4 to 5.5 mm. long. (Subgenus *Pseudornithomyia*) 2
- Ocelli distinct, though sometimes small. Prosternal lobes relatively shorter and wider, more rounded at tips 3
2. Interocular face nearly twice the width of an eye in both sexes. Inner orbit about half as wide as mediovertex, greatly narrowed at lunula. Scutellum with a præapical row of 8 to 14 bristles; disk with many long and short setae, those near the scuto-scutellar suture in an irregular row. Venter of female apically with only a few short and long setae inserted on knobs *O. ambigua*
- Interocular face nearly four times as wide as an eye in both sexes. Inner orbit about half as wide as mediovertex, only slightly narrowed at lunula. Scutellum with a præapical row of 10 to 14 bristles; disk with few setae, none forming a row near scuto-scutellar suture. Venter of female apically with many short and long setae inserted on knobs *O. hoffmannae*
3. Head in front view about as high as wide or slightly higher, nearly circular. Eyes short, less than three times as long as wide. Upper orbit (measured behind the middle of the eye) at least as long as greatest width of inner orbit. Palpi about as long as antenna. Ocelli small; anterior ocellus placed on or above a line drawn along the upper margins of both eyes. Interocular face at least twice the width of an eye in both sexes. Orbital bristles in one continuous row from frontal suture to middle of mediovertex. Scutellum with setulose disk and a præapical row of 6 to 10 bristles.

Nearly apical two-thirds of wing membrane covered with microtrichia. Wing 4 to 5.5 mm. long *O. biloba*

Head in front view slightly to decidedly wider than high, transversely elliptical. Eyes relatively long. Upper orbit (measured behind the middle of the eye) shorter than greatest width of inner orbit. Palpi shorter than antenna. Anterior ocellus placed near or below a line drawn along the upper margins of both eyes. Row of orbital bristles forming two disconnected groups, one near middle of mediovertex, the other along frontal suture. Disk of scutellum with few or no setae before the preapical row of bristles. Wing with microtrichia only over most of first posterior, apex of submarginal and sometimes narrow streaks in second posterior cells; rarely with traces elsewhere 4

4. Interocular face at its narrowest twice as wide as an eye in both sexes; at its widest (near postvertex) wider than the length of an eye. Scutellum with a preapical row of 4 to 6 bristles. Small species; wing 4.5 to 6 mm. long *O. parva*

Interocular face at its narrowest less than twice the width of an eye in both sexes, somewhat narrower in male than in female; at its widest (near postvertex) about as wide as or slightly narrower than the length of an eye 5

5. Larger species; wing 6 to 7.5 mm. long. Scutellum with a preapical row of 6 to 10 (usually 8) bristles *O. avicularia*
Smaller species; wing 4 to 5.5 mm. long. Scutellum with a preapical row of 2 to 6 (usually 4) bristles *O. fringillina*

The Old World *O. avicularia* and *O. biloba*, which do not occur in America, are included in the foregoing key in order to clarify the extralimital affinities of the American species. *O. avicularia* has often been cited from the New World, but in my opinion always by error. At any rate, all the specimens so determined which I have verified, were either *O. fringillina* (in North America) or *O. parva* (in temperate South America).

In 1951a (p. 8) I included *Ornithomyia biloba* Dufour in a list of Chilean Hippoboscidae, on the strength of a fly found labelled "Valparaiso, on *Turdus falklandicus*." As there is no other evidence that this Old World species occurs in America and particularly in view of the wholly improbable host, I now believe that the specimen originated in Europe and received the Chilean label through some oversight. For the time being it is advisable to omit it from a revision of the American hippoboscids.

The following species should be deleted from the list of American Hippoboscidae: *Ornithomyia fuscipennis* Bigot, 1885 (p. 242; no sex; no host. "Colombia"). This insect was for many years very puzzling, particularly as no specimen of *Ornithomyia* agreeing with it had been found since in tropical America. In 1951 I was able to study the female type in the Bigot collection (now the property of Mr. J. E. Collin), where Bigot had labelled it *O. fuscicornis*. It is a true *Ornithomyia* related to *O. avicularia*, though distinct: it is much larger, the wing being 8 mm. long; head broader than high, with a narrow, almost parallel-sided interocular face (very slightly wider than one eye); ocelli large; inner orbit at postvertex less than half as wide as mediovertex. In all these characters the fly agrees well, upon comparison, with specimens of the large Australian species which Speiser (1902a, p. 331) described as *Ornithomyia perfuga*. Speiser (1902b, p. 167), who also saw the type, recognized that it was most nearly related to his *perfuga*, from which he thought it differed in "the somewhat more slender and especially more pointed humeral callosities, and in the costa being yellowish-brown instead of blackish-brown (like the remaining veins), particularly between the tips of subcostalis [subcosta] and radialis [2nd longitudinal]." These differences are of little value and fall within the range of intraspecific variation in *Ornithomyia*. I consider that *Ornithomyia fuscipennis* Bigot is the older, correct name of the Australian fly known hitherto as *O. perfuga* Speiser.

Subgenus *Ornithomyia*, proper

Ocelli present, either well developed or more or less reduced; but at least traces of one or more of them present. Prosternal lobes relatively short and wide, rather bluntly pointed.

The subgenus occurs in both the Old and the New World and comprises the majority of the species, which form two natural groups. The less evolved forms of the group of *O. avicularia* (Linnaeus, 1758) have the head broader than high, with large eyes, always distinct, functional ocelli, normal wings, rather short humeral callosities and a moderately hirsute body. This group contains also the two American species and the Australian *O. fuscipennis* Bigot (1885) (= *O. perfuga* Speiser, 1902). The group of *O. biloba* Dufour (1827), restricted to the Old World, is more specialized, with a lengthened, subcircular head, smaller eyes, ocelli reduced in size or more or less rudimentary, prominent humeral callosities, shorter and broader wings with more crowded veins, and a very hirsute body. Here belong also *O. fur* Schiner

(1868), *O. comosa* Austen (1930), *O. inocellata* Ferris (1930, with partly aborted ocelli) and an undescribed Australian species. The species of the *avicularia* group each breed on a variety of unrelated hosts, while those of the *biloba* group are all specific parasites of swallows (Hirundinidae).

Ornithomyia fringillina Curtis

Figs. 12K, 13A, 19, 20, 27, 28A-L, and 29A-F

Ornithomyia fringillina "A. Matthews, MS" Curtis, 1836, British Entomology, 8, Pl. 585, colored fig. and figs. 2, 3, 4, 8; with letterpress (no sex. England: Weston on the Green near Oxford; on "yellow hammer" [*Emberiza c. citrinella*], "greater titmouse" [*Parus major newtoni*], and "robin" [*Erithacus rubecula melophilus*]; with references to "Curtis, Guide Gen. 1356.4"³⁰ and doubtfully to Degeer's Pl. 16, figs. 21-27. One ♀ type now at the Australian National Museum, Melbourne; others presumably lost). Thompson, 1936, Ent. Mo. Mag., 72, p. 91 (notes on one of Curtis' types); 1936, Ann. Mag. Nat. Hist., (10), 18, p. 310 (Martha's Vineyard, Massachusetts, on *Melospiza m. melodia*, with Mallophaga attached. Elmhurst, New York, on *Turdus m. migratorius*, with Mallophaga attached); 1937, *Op. cit.*, (10), 20, p. 441 (Anticosti I., Quebec, on *Perisoreus c. canadensis*, with *Brüelia* attached. Vancouver, on *Hylocichla u. ustulata*, with *Brüelia interposita* attached. Spruce Brook, Newfoundland, on *Hylocichla f. fuscescens*, with *Brüelia* attached). Strickland, 1938, Canad. J. Res., Sect. D, 16, p. 219 (Alberta: on *Penthestes h. hudsonicus*, *Hesperiphona v. vespertina*, *Picoides arc-ticus*, *Lanius ludovicianus excubitorides*, and several species of sparrows). Spencer, 1938, Proc. Ent. Soc. British Columbia, 34, pp. 42-43 (British Columbia: Chezakut Lake, on *Larus delawarensis*; Lytton, on *Dendragapus obscurus richardsoni*; Lone Butte, possibly on *Dendragapus obscurus richardsoni*; Wentworth, on *Canachites franklinii*; Salmon Arm, on *Accipiter striatus velox*; Jesmond, on hawk; Pitt River, on *Glaucidium gnoma californicum*; Vancouver, on *Asio wilsonianus*, *Dendrocopos pubescens gairdnerii*, *Colaptes c. cafer*, *Junco o. oregonus*, *Melospiza melodia morphna*, *Melospiza lincolni* *gracilis*, *Hedymeles m. melanocephalus*, *Vermivora celata lutescens*, *Passer d. domesticus*, *Hylocichla u. ustulata*, *Acridotheres c. cristatellus*, *Turdus migratorius propinquus*, and *Hylocichla g. guttata*. Infestation with mites. *Brüelia interposita* attached to a fly on *Hylocichla u. ustulata*). Procter, 1946, Biol. Surv. Mt. Desert, 7, Insect Fauna, p. 437 (Maine: Mt. Desert). J. Bequaert and M. Leclercq, 1947, Bull. Ann. Soc. Ent. Belgique, 83, pp. 81 and 83. MacArthur, 1948, Bull. Publ. Mus. Milwaukee, 8, pt. 4, p. 397, figs. 233, 235, and 237 (Illinois: Blue Island, on *Junco h. hyemalis*, *Melospiza g. georgiana*, *M. l. lincolni*, and *Zonotrichia albicollis*. Michigan: McMillan, Luce Co., on *Spizella p. passerina*, *Molothrus a. ater*, and *Passerculus sandwichensis savanna*; Umadilla, Washburn Co., on *Richmondia c.*

³⁰ Bezzi and others date the trivial name *fringillina* by error from 1824, the year when Curtis started the publication of his "British Entomology;" but the letterpress to Pl. 585 is dated 1836. Curtis' reference is to the 2nd edition of his "Guide to an Arrangement of British Insects," Column 278 (1837); the name is not mentioned in the 1st Ed. (1829-1831).

- cardinalis*. Minnesota: without precise locality, on *Plectrophenax nivalis*. Wisconsin: without precise locality, on *Hylocichla guttata faxoni* and *Melospiza m. melodia*; Milwaukee Co., on *Zonotrichia albicollis* and *Richmondia c. cardinalis*; Cedar Grove, Sheboygan Co., on *Falco c. columbarius* and *Zonotrichia albicollis*; Lost Lake, Vilas Co., on *Melospiza g. georgiana*; Door Co.; Madison, Dane Co., on *Turdus m. migratorius*. J. Bequaert, 1950, *Psyche*, 57, p. 113. de Buen, 1950, *An. Inst. Biología, México*, 21, pt. 2, p. 416 (Mexico: Temamatla, 2200 m., 35 Kilom. S. E. of Mexico City, State of Mexico, on *Carpodacus m. mexicanus*). Eliz. Boyd, 1951, *Jl. of Parasitology*, 37, p. 61 (New York State: on *Sturnus v. vulgaris*). Strickland, 1953, *Canad. Jl. Zool.*, 31, No. 3, p. 291 (ptilinum). Thompson, 1954, *Ann. Mag. Nat. Hist.*, (12), 7, p. 19, figs. 1, 2, 6, and 10 (redescription of one of Curtis' types).
- Ornithomyia fringillaria* Wood, 1872, *Insects at Home*, pp. 640 and 659, cut LXXVI, figs. 2 and 2c-d (error for *fringillina*). Clay and Meinertzhagen, 1943, *Parasitology*, 35, pts. 1-2, p. 14 (Massachusetts: without precise locality, on *Turdus m. migratorius*, carrying 2 Mallophaga, *Philopterus* sp.).
- Ornithomyia fringillae* Bagnall, 1926, *Vasculum*, 12, p. 80 (error for *fringillina*).
- Ornithomyia fringilla* Owen, 1953, *Entomologist's Record*, 65, p. 31 (error for *fringillina*).
- Ornithomyia avicularia* Leach, 1817, *Gen. Spec. Eproboscideous Ins.*, pp. 7 and 15; Pl. 25, figs. 4-5 (common in France; in England on "*Tetrao tetrix*" [*Lyrurus tetrix britannicus*] and "*Alauda pipit*" [*Anthus pratensis*]; collected in December in "Danmonia Meridionali" [Devonshire]) [1818, *Mem. Werner. Nat. Hist. Soc.*, Edinburgh, 2, pp. 553 and 561; Pl. 25, figs. 4-5]. van der Wulp, 1869, *Tijdschr. v. Entom.*, 12, p. 80 (Wisconsin). Osten Sacken, 1878, *Smithson. Misc. Coll.*, No. 270, p. 213. Howard, 1883, *South Carolina, Resources and Population*, p. 275. Aldrich, 1905, *Smithson. Misc. Coll.*, 46, No. 1444, p. 654. Washburn, 1905, *Univ. Minnesota, Agric. Expt. Sta., Bull.* 93, p. 163 (Minnesota: on *Junco h. hyemalis*). Speiser, 1907, *Ent. News*, 18, p. 103. Coquillett, 1907, *Op. cit.*, 18, p. 290. Ferris and Cole, 1922, *Parasitology*, 14, pt. 2, p. 199, figs. 15 and 16A-B (♀♂. State of Washington: Keyport. California: Pacific Grove, on *Sayornis s. saya*. Oregon: Upper Alsea River Valley, on *Cyanocitta stelleri frontalis*). McAtee, 1922, *Ent. News*, 33, p. 90 (Oregon: Ontario, on *Corvus brachyrhynchos hesperis*, with Mallophagan attached. Saskatchewan: Macfarlane River, Lake Athabaska, with Mallophagan attached). Cole, 1923, *Ent. News*, 34, p. 950. Falcoz, 1926, *Faune de France*, 14, p. 25, figs. 37, 38, 41, and 42 (in part: figs. copied from Ferris and Cole, 1922). Ferris, 1927, *Canad. Entom.*, 59, p. 251 (California: Baldwin Lake, on *Myadestes townsendi*; La Honda, San Mateo Co., on *Glaucidium gnoma californicum*. British Columbia: Vancouver, on "tanager" and *Sturnus v. vulgaris*). Ewing, 1927, *Ann. Ent. Soc. America*, 20, p. 247, fig. 1 (Ohio: Gates Mills, on *Melospiza m. melodia* and *Dumetella carolinensis*, in both cases with *Brüelia interposita* attached). Spencer, 1928, *Canad. Entom.*, 60, p. 257 (British Columbia: Tofino on Clayoquot Sound, on *Cyanocitta s. stelleri*, with *Brüelia deficiens* attached). Peters, 1933, *Bird-Banding*, 4, p. 71 (New Hampshire: East Westmoreland, on *Sitta c. carolinensis*, *Seiurus n. noveboracensis*, *Geothlypis trichas brachidactyla*, *Spizella p. passerina*, *Melospiza g. georgiana*, and *Melospiza m. melodia*; Peterboro, on *Molothrus a. ater*, *Carpodacus p. purpureus*, *Junco h. hyemalis*, *Spizella p. passerina*, *Zonotrichia albicollis*, and *Melospiza m. melodia*. Massachusetts: Worcester, on *Dumetella carolinensis*, *Hylocichla f. fuscescens*, *Agelaius p. phoeniceus*, *Icterus galbula*, *Passerculus sandwichensis savanna*, *Zonotrichia albicollis*, and *Melospiza m. melodia*; Groton, on *Dumetella caro-*

- linensis*, *Quiscalus q. quiscula*, and *Melospiza m. melodia*; Oak Bluffs, on *Icterus galbula*, *Molothrus a. ater*, *Pipilo e. erythrophthalmus*, and *Melospiza m. melodia*. Vermont: Wells River, on *Zonotrichia albicollis* and *Dumetella carolinensis*. New York: Elmhurst, Long Island, on *Toxostoma r. rufum*, *Hylocichla f. fuscescens*, *Dendroica coronata*, and *Zonotrichia albicollis*; Mohonk Lake, on *Turdus m. migratorius*, *Piranga erythromelas*, *Pipilo e. erythrophthalmus*, *Junco h. hyemalis*, *Zonotrichia albicollis*, and *Melospiza m. melodia*. Ohio: Leetonia, on *Turdus m. migratorius*, *Melospiza m. melodia*, and *Spizella p. pusilla*; Gates Mills, on *Melospiza m. melodia*; Columbus, on *Melospiza m. melodia*. Michigan: McMillan, on *Molothrus a. ater*, *Passerculus sandwichensis savanna*, *Poocetes g. gramineus*, and *Spizella p. passerina*. Eidmann, 1935, Arb. Morphol. Taxon. Entom., Berlin-Dahlem, 2, p. 99 (Labrador: Upper Matamek River, 50° 17' N., 65° 68' W., on *Junco h. hyemalis*, August 22). Spencer, 1938, Proc. Ent. Soc. British Columbia, 34, p. 42. Not of Linnaeus, 1758.
- Ornithomyia aviculare* Clay and Meinertzhagen, 1943, Parasitology, 35, pts. 1-2, p. 12 (in part: specimens from North America previously reported as carrying Mallophaga). Error for *O. avicularia*, but not Linnaeus' species.
- Ornithomyia pallida* Say, 1823, Jl. Ac. Nat. Sci. Philadelphia, 3, p. 103 (no sex; on "*Sylvia sialis*" [*Siala s. sialis*]). United States, without precise locality. Type lost); 1837, Oeuvres Entomologiques, edit. by Gory, p. 103; 1859, Complete Writings, edit. by LeConte, 2, p. 87. Wiedemann, 1830, Aussereurop. Zweifl. Ins., 2, p. 610. Walker, 1849, List Dipt. Brit. Mus., 4, p. 1143 (Nova Scotia). Osten Sacken, 1858, Cat. Dipt. North America, p. 86; 1878, Smithsonian. Misc. Coll., No. 270, p. 213. Rondani, 1878, Ann. Mus. Civ. Stor. Nat. Genova, 12, p. 159 (Mexico). Brodie and White, 1883, Check List Ins. Dom. Canada, p. 57. Howard, 1883, South Carolina, Resources and Population, p. 275. Johnson, 1900, 27th Ann. Rept. New Jersey State Bd. Agric., (for 1899), p. 699 (New Jersey: Delaware River, on *Dolichonyx oryzivorus* and *Agelaius p. phoeniceus*). Aldrich, 1905, Smithsonian. Misc. Coll., 46, No. 1444, p. 654. Not *O. pallida* Latreille, 1812, nor of v. Olfers, 1816.
- Ornithomyia anchineuria* Speiser, 1905, Zeitschr. Syst. Hym. Dipt., 5, p. 348 (new name for *Ornithomyia pallida* Say, 1823); 1907, Ent. News, 18, p. 103; 1908, Zeitschr. Wiss. Insektenbiol., 4, p. 303. Johnson, 1910, Ann. Rept. New Jersey State Mus., (for 1909), p. 814; 1913, Bull. Amer. Mus. Nat. Hist., 32, p. 90 (in list of Florida Diptera, but not actually taken there). Davis, 1922, Proc. Staten Island Inst. Arts Sci., 1, p. 64 (New York: Yankee Lake, Wurtsboro, Sullivan Co., on *Geothlypis t. trichas*; Richmond, Staten Island, on *Thryothorus l. ludovicianus*). Johnson, 1922, Psyche, 29, p. 81 (Pennsylvania: Clifton, on *Hylocichla guttata faxoni*. Massachusetts: Southbridge, on *Turdus m. migratorius*; Worthington, on *Dumetella carolinensis*; Essex, on *Passerculus sandwichensis savanna*. Vermont: Woodstock, on *Junco h. hyemalis*. Quebec: Ellis Bay, Anticosti I., on *Perisoreus c. canadensis* [as "*P. barbouri*"], with Mallophaga attached. Ontario: North Bay, on *Loxia curvirostra pusilla*); 1925, Occ. Papers Boston Soc. Nat. Hist., 7, p. 293 (Maine: Bar Harbor. New Hampshire: Peterboro, on *Melospiza m. melodia*. Vermont: Chittenden, on *Spizella p. passerina*. Massachusetts: Chilmark, on *Melospiza m. melodia*); 1925, Bull. Northeastern Bird-Banding Assoc., 1, p. 52; 1929, *Op. cit.*, 5, p. 49 (Massachusetts: Rock, on *Spizella p. passerina*; Concord, on *Melospiza m. melodia*; Martha's Vineyard, on *Melospiza m. melodia* and *Pipilo e. erythrophthalmus*; Athol, on *Carduelis p. purpureus*; Wellesley, on *Hedymeles ludovicianus*; Needham, on *Molothrus a. ater*; Holbrook, on *Toxostoma r. rufum*. New Hampshire: Peterboro, on *Spizella p. passerina* and *Dendrocopos pubescens*

- medianus*. Vermont: Wells River, on *Spizella p. passerina* and *Melospiza m. melodia*. Maine: Soldier Pond, on *Junco h. hyemalis*. Pennsylvania: Philadelphia, on *Dolichonyx oryzivorus* and *Agelaius p. phoeniceus* [evidently the same specimens as his Delaware River, New Jersey, records of 1900]; 1930, Publ. Nantucket M. Mitchell Assoc., 3, No. 2, p. 158 (in Nantucket list, but not actually taken there). Peters, 1936, Bird-Banding, 7, pp. 14, 19, 20, 21, 22, 23, 24, 25, 26, and 27 (Maine: on *Junco h. hyemalis*. New Hampshire: on *Dendrocopos pubescens medianus*, *Sitta c. carolinensis*, *Dumetella carolinensis*, *Turdus m. migratorius*, *Hylocichla f. fuscescens*, *Siala s. sialis*, *Seiurus n. noveboracensis*, *Geothlypis trichas brachidactyla*, *Molothrus a. ater*, *Carpodacus p. purpureus*, *Junco h. hyemalis*, *Spizella p. passerina*, *Zonotrichia albicollis*, *Melospiza l. lincolni*, *Melospiza g. georgiana*, and *Melospiza m. melodia*. Vermont: on *Dumetella carolinensis*, *Passerculus sandwichensis savanna*, and *Zonotrichia albicollis*. Massachusetts: on *Dumetella carolinensis*, *Turdus m. migratorius*, *Quiscalus q. quiscula*, *Molothrus a. ater*, *Carpodacus p. purpureus*, *Hedymeles ludovicianus*, *Passerculus sandwichensis savanna*, *Spizella p. passerina*, *Zonotrichia albicollis*, and *Melospiza m. melodia*. Connecticut: on *Dumetella carolinensis*, *Hylocichla f. fuscescens*, *Agelaius p. phoeniceus*, *Icterus galbula*, *Passerculus sandwichensis savanna*, and *Melospiza m. melodia*. New York: on *Dumetella carolinensis*, *Toxostoma r. rufum*, *Turdus m. migratorius*, *Hylocichla guttata faxonii*, *Hylocichla ustulata swainsoni*, *Hylocichla f. fuscescens*, *Dendroica coronata*, *Piranga erythromelas*, *Pipilo e. erythrophthalmus*, *Junco h. hyemalis*, *Zonotrichia albicollis*, and *Melospiza m. melodia*. Pennsylvania: on *Colinus v. virginianus*. Maryland: on *Wilsonia citrina* and *Zonotrichia albicollis*. Ohio: on *Turdus m. migratorius*, *Molothrus a. ater*, *Richmondia c. cardinalis*, *Spizella p. pusilla*, and *Melospiza m. melodia*. Michigan: on *Molothrus a. ater*, *Passerculus sandwichensis savanna*, *Poocetes g. gramineus*, and *Spizella p. passerina*). Herman, 1937, Bird-Banding, 8, pp. 127 and 163 (Massachusetts: North Eastham, on *Molothrus a. ater*, with *Mallophaga* attached, and on *Circus cyaneus hudsonius*, *Tyrannus tyrannus*, *Penthestes a. atricapillus*, *Dumetella carolinensis*, *Turdus m. migratorius*, *Siala s. sialis*, *Dendroica a. aestiva*, *Dendroica p. pinus*, *Geothlypis trichas brachidactyla*, *Agelaius p. phoeniceus*, *Pipilo e. erythrophthalmus*, *Passerculus sandwichensis savanna*, *Ammodramus savannarum australis*, *Poocetes g. gramineus*, *Spizella p. passerina*, *Spizella p. pusilla*, and *Melospiza m. melodia*. Infestation with mites). Procter, 1938, Biol. Surv. Mt. Desert, 6, Insect Fauna, p. 378 (Maine: Bar Harbor). Herman, 1945, California Fish Game, 31, p. 22, figs. 11A-B (puparium). Procter, 1946, Biol. Surv. Mt. Desert, 7, Insect Fauna, p. 437. Thompson, 1947, Ent. Mo. Mag., 83, p. 212.
- Ornithomyia anchineura* Coquillett, 1907, Ent. News, 18, p. 290 (error for *anchineuria*; from Washington, D. C. to California). Cole and Lovett, 1921, Proc. California Ac. Sci., (4), 11, p. 344 (Oregon: Upper Alsea Valley, Benton Co., on *Cyanocitta stelleri frontalis*). Johannsen, 1928, in Leonard, Cornell Univ. Agric. Expt. Sta., Mem. 101, (for 1926), p. 868 (New York: Port Jefferson, Long Island, on *Toxostoma r. rufum*). Beer, 1944, Jl. Wildlife Manag., 8, p. 91 (State of Washington: Okanogan Co., on *Dendragapus obscurus richardsoni*).
- Ornithomyia avicularia anchineuria* Eichler, 1937, Mitt. Ver. Sächsischer Ornith., 5, pt. 3, p. 129.
- Ornithomyia chloropus* Bergroth, 1901, Medd. Soc. Fauna Flora Fennica, 26, p. 146 (no sex. Finland: Tammela in southern Fennia, 2 cotypes on "*Asio accipitrinus* Pallas" [*Asio f. flammeus*]. Present location of types unknown). Falcoz, 1930, Encyclop. Entom., Sér. B, Diptera, 5, (for 1929), p. 33 (St. Pierre-and-Miquelon). Stackelberg, 1933, Tabl. Anal. Faune URSS, No. 7, Mouches Partie Européenne de l'URSS, p. 481.

Ornithomyia lagopodis Sharp, 1907, Ent. Mo. Mag., 43, p. 59 (♀ ♂. Scotland: Nethy Bridge, Inverness-shire; Boat O'Garten; Caithness; Blair Atholl, North Perthshire; all on *Lagopus scoticus*. Also Norway, on "*Lagopus albus*" [*Lagopus lagopus*]; "will bite human beings." Two ♀ ♀ from Caithness at Brit. Mus. are marked as "types"). Shipley, 1909, Proc. Zool. Soc. London, pp. 321-322; Pl. 43, figs. 21A-B; Pl. 44, figs. 22-25 (♀ ♂, puparium).

Ornithomyia lagopodis S. Smith, 1950, The Yellow Wagtail, p. 149 (error for *lagopodis*).

Ornithomyia sp. Elliott and Dearnness, 1899, 29th Rept. Ent. Soc. Ontario, (for 1898), p. 60, figs. 33-34 (Ontario: Bryanton, on *Zonotrichia albicollis*. Puparium). Banks, 1920, Psyche, 27, p. 20 (Anticosti I., Quebec, with Mallophaga attached).

Although *Ornithomyia fringillarum* Stadler (1948) was no doubt an error for *O. fringillina*, the author applied the name to specimens of *O. biloba* Dufour, from swallows, and it should be listed in the synonymy of that species.

Distribution and Specimens Examined. ALASKA: Crater Mt., 62° 48' N., 156° 49' W., on *Surnia ulula caparoch*, Aug. 20, and *Falco columbarius bendirei*, Aug. 12 (A.H. Twitchell); Takotna, 63° N., 156° W., on *Canachites c. canadensis*, Oct. 1 (A.H. Twitchell); Nelchina River, near Mt. Witherspoon, N.W. of Valdez, 61° 30' to 62° N., 147° W., Aug. 26 (R.B. Williams); 10 miles W. of Paxson, about 63° N., 146° W., on *Anthus spinoletta rubescens*, Sept. 7, 1952 (G.D. Gill); Fairbanks, 64° 59' N., 148° 10' W., 3 flies on *Bonasa umbellus yukonensis*, June 19 (Arctic Aëromedical Lab.).

DOMINION OF CANADA. ALBERTA (recorded by Strickland, 1938): Ft. Chipewyan, Athabaska Delta (F. Harper); Belvedere, on *Penthestes h. hudsonicus*, *Zonotrichia leucophrys gambelii*, *Picoides arcticus*, *Turdus m. migratorius*, and *Hesperiphona v. vespertina* (C.G. Harrold); Edmonton, on *Lanius ludovicianus excubitorides* (E.H. Strickland); Tilley (R.W. Salt); Red Deer River, on *Turdus m. migratorius*. — BRITISH COLUMBIA (recorded by Ferris, 1927; Spencer, 1928, 1938; Thompson, 1937): Vancouver, on *Colaptes c. cafer*, *Melospiza lincolni gracilis*, *Vermivora celata lutescens*, *Acridotheres c. cristatellus*, *Hylocichla u. ustulata* (carrying 4 ♀ and one immature Mallophaga), *Turdus migratorius propinquus*, *Melospiza melodia morphna*, *Dendrocopos pubescens gairdnerii*, *Passer d. domesticus*, *Hylocichla g. guttata*, *Hedymeles m. melanocephalus*, and *Junco o. oreganus* (R.A. Cumming), and on *Piranga ludoviciana*; Kamloops, on *Dendragapus obscurus fuliginosus* (E.R. Buckell); Quesnel, on *Accipiter cooperii* (J. Grant); probably Vancouver, on *Asio wilsonianus*, Feb., newly-emerged fly carrying about its puparium (K. Racey); Chezakut Lake, on *Larus delawarensis* (R.A. Cumming); Trinity Valley, on *Canachites franklinii* (J. Grant); Upper Pitt River, on *Glaucidium gnoma californicum* (R.A. Cumming); Turner Valley, on *Falco s.*

sparverius and *Bonasa umbellus togata* (J. Grant); Wentworth, on *Canachites franklinii* (K. Racey); Lytton, on *Dendragapus obscurus richardsoni* (J.A. Munro), *Bonasa umbellus umbelloides* (A. Brooks), and *Hesperiphona vespertina brooksi*; McLeese Lake, July 7, 3 ♂ on *Sphyrapicus varius ruber* (T.R. Howell); Quinsam Lake, Vancouver I., on *Dendragapus obscurus fuliginosus* and *Zonotrichia leucophrys pugetensis* (J.S.F. Bendell); Barriere, on *Dendragapus obscurus richardsoni* (L. Proulx); Grindrod, in house, March 15, and on 2 *Loxia curvirostra bendirei*, *Dendrocopos pubescens leucurus*, *Falco s. sparverius*, *Molothrus ater artemisiae*, and *Piranga ludoviciana* (J. Wynne); Alta Lake, on *Zonotrichia albicollis* (I.McT. Cowan); Okanagan Landing, on *Hesperiphona vespertina brooksi*, Sept. 15 (F.C. Bishopp); Horse Lake, Lone Butte (W.R.W.); Salmon Arm, on *Accipiter striatus velox* (E.R. Buckell); Deadman's Creek, on *Lagopus l. lagopus* (= *albus*) (J. Grant); Bridge Lake, Bridge Creek, on *Canachites franklinii*, Oct. 13 (P. Martin). — LABRADOR (recorded by Eidmann, 1935): Goose Bay, 53° 20' N., 60° 20' W., Sept. 26 (R. Traub). — NEWFOUNDLAND (recorded by Thompson, 1937): Spruce Brook, on *Hylocichla ustulata swainsoni*, Sept., and *Hylocichla f. fuscescens*, Sept., the latter with a Mallophagan attached (G.K. Noble). — NOVA SCOTIA (recorded by Walker, 1849): without precise locality (Redman); Wolfville, on *Spizella p. passerina*, Sept. 11, and *Junco h. hyemalis* (R.W. Tufts). — ONTARIO (recorded by Elliott and Dearness, 1899; Johnson, 1922, 1929): Macdiarmid, Lake Nipigon, on *Vermivora peregrina* (N.K. Bigelow); Roebuck, on *Turdus m. migratorius* (G.H. Hammond); Smoky Falls near Kapuskasing, on *Carpodacus p. purpureus* and *Zonotrichia albicollis* (R.V. Whelan); Murillo, on *Molothrus a. ater* (T.M. Shortt); Ottawa, on *Melospiza m. melodia* (R.E. DeLong); Brulé Point, 4 flies on a nestling of *Hesperiphona v. vespertina* (C.H.D. Clarke); North Bay, on *Loxia curvirostra pusilla*, Sept. 7 (G.S. Miller, Jr.); Pan-cake Bay, Algoma District, on *Bubo v. virginianus*, *Melospiza m. melodia*, and 3 *Hesperiphona v. vespertina* (G.H.D. Clarke); Brulé Lake, Algonquin Park, on *Zonotrichia albicollis*, *Hesperiphona v. vespertina*, *Euphagus carolinus*, *Sphyrapicus v. varius*, and *Picoides arcticus* (G.H.D. Clarke); Pointe Pelée, on *Philohela minor* (A.W. Andrews); Agawa Bay, Lake Superior, on *Penthestes h. hudsonicus* and *Melospiza m. melodia* (W.G. Fargo); Toronto, on *Zonotrichia albicollis*, *Dendroica tigrina*, *Dendroica castanea*, *Toxostoma r. rufum*, and *Passer d. domesticus* (R.S. Baker); Lake of Two Rivers, Algonquin Park, on *Melospiza m. melodia*, with

Mallophagan attached, *Zonotrichia albicollis*, and *Spizella p. passerina* (D.M. Davies); Lake Sasajewan, Algonquin Park, on *Melospiza m. melodia* and *Zonotrichia albicollis* (D.M. Davies). — QUEBEC (recorded by Banks, 1920; Johnson, 1922, 1929; Thompson, 1937): Ellis Bay, Anticosti I., Sept. 3, on *Perisoreus c. canadensis*, with two Mallophaga (*Brüelia* sp.) attached (W.S. Brooks. — Case reported by N. Banks, 1920); St. Anne's, on *Molothrus a. ater* (W. E. Whitehead); Montebello, on *Megaceryle a. alcyon* (W.E. Whitehead); Joliette, on *Pandion haliaetus carolinensis* (J. Ouellet); Chateauguay River, on *Philohela minor*, Sept. 22 (Lionel Philippe). — SASKATCHEWAN (recorded by McAtee, 1922): Macrorie, on *Molothrus a. ater*, *Turdus m. migratorius*, and *Agelaius p. phoeniceus* (F.J.H. Fredeen); Poplar Point, Lake Athabaska (F. Harper); mouth of Macfarlane River, Lake Athabaska, bearing a Mallophagan, *Brüelia rotundata* (F. Harper); Lobstick I., Lake Athabaska, Aug. 20 (F. Harper); Island 1 mile E. of Cracklingstone Pt., Lake Athabaska, Aug. 17 (F. Harper). — YUKON: Timber Creek, a tributary of the Old Crow River, up river from Black Fox Creek, about 68° N., 140° W., July 30 (O.J. Murie).

ST. PIERRE-AND-MIQUELON (recorded by Falcoz, 1930): specimens at Paris Museum (Baron, 1890).

UNITED STATES. ARIZONA: Betatakin Beko, N.W. of Kayenta, Navajo Co., 7000 ft. on *Junco mearnsi* (A.R. Phillips); Cassadore Spring, 15 miles N. of San Carlos, Gila Co., on *Otus asio mecallii* (A.R. Phillips). — CALIFORNIA (recorded by Ferris and Cole, 1922; Ferris, 1927): Berkeley, Alameda Co., on *Pipilo maculatus falcifer* (E.L. Sumner; H.E. Childs, Jr., Aug. 28, fly with Mallophagan attached; B.F. Brown, Aug. 30; and O.E. Sousa), on *Melospiza melodia gouldii* (O.E. Sousa; S.K. Carnie, Oct. 6), on *Zonotrichia leucophrys nuttalli* (H.E. Childs, Jr.), on *Carpodacus mexicanus frontalis* (I.B. Tarshis), on *Zonotrichia coronata*, Oct. 12, with Mallophagan attached, *Passerella iliaca* subsp., Nov. 15, and *Aphelecoma c. californica*, Nov. 1 (S.K. Carnie), on *Pipilo fuscus petulans* (H.E. Childs, Jr., 1 fly; O.E. Sousa, 2 flies, one with Mallophagan attached), and on *Baeolophus i. inornatus* (D.W. Johnston); San Francisco, on *Zonotrichia leucophrys nuttalli* (McGregor), and on *Falco s. sparverius* and *Thryomanes bewickii spilurus* (G.D. Hanna); Carmel, Monterey Co., on *Zonotrichia coronata* (L.O. Williams); Pacific Grove, Monterey Co., on *Penthestes rufescens barlowi*, Dec. 28 (A.K. Fisher) and on *Sayornis s. saya*; La Honda, San Mateo Co., on *Glaucidium gnoma californicum*; Baldwin Lake, San Bernardino Co., on *Myadestes townsendi*; Mill Valley, Marin

Co. (E.S. Ross); Woodacre, Marin Co., on *Zonotrichia coronata*, two flies with Mallophaga (*Brüelia* sp.) attached (J. Maillard); Hastings Reservation near Jamesburg, Monterey Co., on *Zonotrichia coronata* (J.M. Linsdale). — COLORADO: Steamboat Springs, Routt Co., on *Icteria virens longicauda* (O. Briant). — CONNECTICUT (recorded by Peters, 1936): Waterford, New London Co. (P. Crowe); Pomfret, Windham Co., on *Hylocichla f. fuscescens*, Aug. 3, *Melospiza m. melodia*, July 3, *Icterus galbula*, July 24, and *Agelaius p. phoeniceus*, Aug. 3 (F.C. Bishopp). — DISTRICT OF COLUMBIA: on *Toxostoma r. rufum*, Oct. 14 (T. Pergande) and on *Cyanocitta c. cristata*, July 18 (J.C. Bridwell). — ILLINOIS (recorded by MacArthur, 1948): Waukegan, Lake Co., on *Zonotrichia albicollis* (W.I. Lyon); Blue Island, Cook Co., on 2 *Junco h. hyemalis*, Oct. 15 and 27, *Melospiza l. lincolnii*, Oct. 10, *Zonotrichia albicollis*, Oct. 20, and *Melospiza g. georgiana*, Oct. 13 (K.E. Bartel). — IOWA: Ames, Story Co., Oct. 18, on a person who handled a live, native species of sparrow (J.L. Krall). — MAINE (recorded by Johnson, 1925, 1929; Peters, 1936; Procter, 1938, 1946): Northeast Harbor, Hancock Co., on *Carpodacus p. purpureus* (H.E. Bailey); Bar Harbor, Hancock Co. (B. Moore); Mt. Desert Island, Hancock Co., on *Hylocichla guttata faxoni*, with two Mallophaga attached, July 29 (A.E. Brower); Soldier Pond, Aroostook Co., on *Junco h. hyemalis*, Sept. 28 (E.O. Grant). — MARYLAND (recorded by Peters, 1936): Laurel, Prince Georges Co., on *Wilsonia citrina*, July 21 (E.B. Marshall); Beltsville, Prince Georges Co., on *Melospiza m. melodia*, July 8, *Turdus m. migratorius*, July 23, and *Spizella p. passerina*, June 28 (F.R. Smith); Patuxent Research Refuge, Bowie, Prince Georges Co., on *Melospiza l. lincolnii* (R.T. Mitchell). — MASSACHUSETTS (recorded by Johnson, 1922, 1925, 1929; Peters, 1933, 1936; Thompson, 1936; Herman, 1937; Clay and Meinertzhagen, 1943): North Eastham, Barnstable Co., on *Circus cyaneus hudsonius*, *Tyrannus tyrannus*, *Penthestes a. atricapillus*, *Dumetella carolinensis*, *Turdus m. migratorius*, *Sialia s. sialis*, *Dendroica a. aestiva*, *Dendroica p. pinus*, *Geothlypis trichas brachidactyla*, *Agelaius p. phoeniceus*, *Molothrus a. ater*, Oct. 3, *Pipilo e. erythrophthalmus*, *Passerculus sandwichensis savanna*, Oct. 18, *Ammodramus savannarum australis*, *Poocetes g. gramineus*, *Spizella p. passerina*, *Spizella p. pusilla*, and *Melospiza m. melodia*, Nov. 6 (C.M. Herman); Sagamore Beach, Barnstable Co., on *Toxostoma r. rufum* (H.S. Fuller); Groton, Middlesex Co., on *Turdus m. migratorius*, *Dumetella carolinensis*, *Passerculus sandwichensis savanna*, *Hylocichla f. fuscescens*, *Zonotrichia albicollis*,

Spizella p. passerina, Oct. 15, *Penthestes a. atricapillus*, *Mniotilta varia*, and *Melospiza m. melodia* (W.P. Wharton); Oak Bluffs, Martha's Vineyard, on *Agelaius p. phoeniceus*, *Melospiza m. melodia*, with Mallophagan (*Brüelia* sp.) attached, *Molothrus a. ater*, *Pipilo e. erythrophthalmus*, and *Vermivora r. ruficapilla* (S. Harris and G.C. Eustis), on *Dumetella carolinensis* (M.M. Cole), and on *Spizella p. passerina*, with Mallophagan (*Brüelia* sp.) attached (F.C. Bishopp); Rock, Littleboro, Plymouth Co., on *Melospiza m. melodia*, *Vermivora r. ruficapilla* and *Spizella p. passerina* (A.W. Higgins); Cohasset, Norfolk Co., on *Spizella p. passerina* (L.B. Fletcher) and *Melospiza m. melodia* (C.L. Whittle); Essex, Essex Co., on *Passerculus sandwichensis savanna* (A.B. Fuller); WORTHINGTON, Hampshire Co., on *Dumetella carolinensis* (Niles); AUBURNDALE, Middlesex Co., on *Cyanocitta c. cristata* (C.B. Floyd); Southbridge, Worcester Co., on *Turdus m. migratorius* (S.W. Bromley); Salem, Essex Co., on *Accipiter cooperii*, Oct. 5 (R.P. Dow); Milton, Norfolk Co., on *Quiscalus quiscula aeneus* (R.M. Hinchman); Hadley, Hampshire Co., on *Melospiza l. lincolni* (J. Baird); Topsfield, Essex Co., on *Spizella a. arborea* (S.K. Harris); Chilmark, Dukes Co., on *Melospiza m. melodia* (S.K. Harris); Concord, Middlesex Co., on *Melospiza m. melodia* (F.B. White; W.E. Schevill); Athol, Worcester Co., on *Carpodacus p. purpureus* (R. Allison); Wellesley, Norfolk Co., on *Hedymeles ludovicianus* (Mrs. H.C. Dunham); Needham, Norfolk Co., on *Molothrus a. ater* (J.D. Smith); Holbrook, Norfolk Co., on *Toxostoma r. rufum* (J.D. Smith); Old Deerfield, Franklin Co., on *Molothrus a. ater* and *Melospiza m. melodia* (Miss Marion E. Smith); Hudson, Middlesex Co. (C.W. Johnson). — MICHIGAN (recorded by Peters, 1933, 1936; MacArthur, 1948): 1 mile S. of Umadilla, Washtenaw Co., on *Richmondia c. cardinalis* (Camburn and Sutton); McMillan, Luce Co., on *Poocetes g. gramineus*, *Quiscalus quiscula aeneus*, 2 *Molothrus a. ater*, July 28 and Aug. 3, *Spizella p. passerina*, July 29, and *Passerculus sandwichensis savanna*, July 23 (O.M. Bryens). — MINNESOTA (recorded by Lugger, 1897; Washburn, 1905; MacArthur, 1948): Pine Co., on *Bonasa u. umbellus* (R.E. Schumacher); Grand Rapids, Itasca Co., on *Junco h. hyemalis*; Hennepin Co. — MONTANA: Bridger Mts., Carbon Co., on *Dendragapus obscurus richardsoni*, Sept. 24 (H.B. Mills); East Fork, Ravalli Co., on *Phasianus colchicus* (J. Brennan); Harlan Gulch, Ravalli Co., on *Bonasa umbellus umbelloides*, Oct. 8, and *Dendragapus obscurus richardsoni*, Aug. 10 (W.L. Jellison); Goat Mountain, Ravalli Co., on *Dendragapus obscurus richardsoni*, Sept. 18 (C.B. Philip);

Beaverhead Co., on *Canachites c. canadensis* (C.B. Philip and W.L. Jellison); Darby, Ravalli Co., on *Cyanocitta c. cristata*, Sept. 2 (V. Bailey); Fisher River, 25 miles S. of Libby, Lincoln Co., on *Bonasa umbellus umbelloides* (Lowell Adams); Bozeman, Gallatin Co., Oct. 8 (C.B. Philip). — NEW HAMPSHIRE (recorded by Johnson, 1925, 1929; Peters, 1933, 1936): East Westmoreland, Cheshire Co., on 2 *Spizella p. passerina*, Aug. 21 and 27, *Sialia s. sialis*, *Hylocichla f. fuscescens*, *Geothlypis t. trichas*, Aug. 24, *Geothlypis trichas brachidactyla*, *Turdus m. migratorius*, *Melospiza l. lincolni*, *Melospiza g. georgiana*, and *Melospiza m. melodia* (L.O. Shelley); Ashland, Grafton Co., on *Melospiza m. melodia* (Mrs. R.B. Harding); Peterboro, Hillsboro Co., on 2 *Melospiza m. melodia*, Aug. 26 and Sept., *Zonotrichia albicollis*, *Junco h. hyemalis*, *Carpodacus p. purpureus*, *Spizella p. passerina*, and *Dendrocopos pubescens medianus* (Mrs. C.L. Whittle). — NEW JERSEY (recorded by Johnson, 1900, 1910): Ridgewood, Bergen Co., on hawk (H. Hales); Tenafly, Bergen Co., on *Melospiza m. melodia* (Mrs. H. Carnes); Demarest, Bergen Co., on *Turdus m. migratorius*, *Cyanocitta c. cristata*, *Dumetella carolinensis*, *Molothrus a. ater*, *Piranga erythromelas*, *Hylocichla mustelina*, *Hylocichla f. fuscescens*, *Seiurus a. aurocapillus*, *Hedymeles ludovicianus*, *Icterus galbula*, *Sitta c. carolinensis*, *Toxostoma r. rufum*, *Baeolophus bicolor*, *Dendroica c. coronata*, *Zonotrichia albicollis*, *Vermivora pinus*, *Quiscalus quiscula aeneus*, *Troglodytes a. aëdon*, *Setophaga ruticilla*, *Geothlypis trichas brachidactyla*, *Melospiza m. melodia*, and *Pipilo e. erythrophthalmus* (B.S. Bowdish; some of these with Mallophaga, as listed in Part I, p. 170); Pequannock, Morris Co., on *Quiscalus q. quiscula* (Mrs. M. Dumont); Stag Lake, Sussex Co., on *Accipiter striatus velox*, Oct. (W.J. McAtee). — NEW MEXICO: Rio Arriba Co., on chickadee (*Penthestes* sp.), nuthatch (*Sitta* sp.) and titmouse (*Baeolophus* sp.) (L.D. Compton); Upper Pecos River, San Miguel Co., on *Dendragapus o. obscurus* (through L. Lee). — NEW YORK (recorded by Davis, 1922; Johannsen, 1928; Peters, 1933, 1936; Thompson, 1936; Boyd, 1951): Delmar, Albany Co., on *Sturnus v. vulgaris*, Oct. 26, *Molothrus a. ater*, July 25, and *Turdus m. migratorius*, July 13 (F.C. Goble); Mohonk Lake, Ulster Co., on *Melospiza m. melodia*, *Junco h. hyemalis*, *Zonotrichia albicollis*, *Turdus m. migratorius*, and *Pipilo e. erythrophthalmus* (D. Smiley, Jr.); Richmond, Staten Island, on *Thryothorus l. ludovicianus* (J.P. Chapin); Orient, Long Island, on *Pipilo e. erythrophthalmus*, June 4 (R. Latham); Elmira, Tompkins Co., on *Sturnus v. vulgaris* (Elizabeth M. Boyd); White Plains, Westchester Co., on *Zono-*

trichia albicollis (C. Farley); Syracuse, Onondaga Co., on *Spizella p. passerina* (R.D. Manwell); Babylon, Long Island (Blanton and Bordera); Port Jefferson, Long Island, on *Toxostoma r. rufum*, July (R.C. Murphy); Elmhurst, Long Island, on *Sitta c. carolinensis*, *Compsothlypis americana pusilla*, *Seiurus a. aurocapillus*, *Zonotrichia albicollis*, *Turdus m. migratorius*, *Hylocichla guttata faxoni*, *Hylocichla ustulata swainsoni*, *Hylocichla f. fuscescens*, *Melospiza g. georgiana*, *Junco h. hyemalis*, *Geothlypis trichas brachidactyla*, *Dendroica c. coronata*, and *Toxostoma r. rufum* (Marie V. Beals); Yankee Lake, Wurtsboro, Sullivan Co., on *Geothlypis t. trichas* (J.P. Chapin); Macedon, Wayne Co., on *Colaptes auratus luteus* (J.D. Hood). — NORTH DAKOTA: Fargo, Cass Co., on *Melospiza l. lincolni* (O.A. Stevens). — OHIO (recorded by Ewing, 1927; Peters, 1933, 1936): Columbus, Franklin Co., on *Turdus m. migratorius* and *Richmondia c. cardinalis* (E.S. Thomas), and on *Zonotrichia albicollis* (W. Jones); Leetonia, Columbiana Co., on *Turdus m. migratorius* and *Spizella p. pusilla*; Gates Mills, Cuyahoga Co., on *Molothrus a. ater*, *Melospiza m. melodia*, and *Dumetella carolinensis* (R. Boulton). — OREGON (recorded by McAtee, 1922; Cole and Lovett, 1921; Ferris and Cole, 1922): without precise locality, on *Colaptes c. cafer*; Ontario, Malheur Co., on *Corvus brachyrhynchos hesperis* (E.R. Kalmbach); Upper Alsea River Valley, Benton Co., on *Cyanocitta stelleri frontalis* (F.R. Cole and A.L. Lovett); 2 miles E. of Union Creek Junction (West slope of Cascade Mts.), 400 ft., Jackson Co., on *Turdus migratorius propinquus* (D.S. Farner); Tillamook, Tillamook Co., on *Sphyrapicus varius ruber*, Dec. 1, and *Carpodacus purpureus californicus*, Aug. 31 (A. Walker); Blaine, Tillamook Co., on *Glaucidium gnoma californicum* (A. Walker); Adel, Lake Co., on *Myadestes townsendi*, Oct. 18 (A. Walker); Netarts, Tillamook Co., on *Junco oreganus shufeldti*, Dec. 1, *Melospiza melodia morphna*, Oct. 18, and *Dendrocopos villosus harrisi*, June 25 (A. Walker); Nehalem, Tillamook Co., on chicken hawk (H.E. Henderson); Euchre Mt., 7 miles N.E. of Siletz, Lincoln Co., on *Cathartes aura teter*, 1 ♀ fly with 4 *Brüelia* sp. attached (Roy Wing); Corvallis, Benton Co., on *Dendrocopos villosus harrisi*; Boyer, 9 flies on *Glaucidium gnoma californicum*, Aug. 16 (J. A. Macnab). — PENNSYLVANIA (recorded by Johnson, 1922, 1929; Peters, 1936): College Station, Easton, Northampton Co., on *Icterus galbula* (Merrill Wood); Philadelphia Neck, South Philadelphia, on 3 *Agelaius p. phoeniceus*, Aug. 19 and 26, and Oct. 18, and 3 *Dolichonyx oryzivorus*, Sept. 2, 11 and 27 (C. Liebeck); Fredericktown, Washington Co., on *Mo-*

lothrus a. ater, July 4, and *Troglodytes a. aëdon*, July 9; Point Pleasant, Bucks Co., on *Richmondia c. cardinalis*; Harrisburg, Dauphin Co., on *Hylocichla mustelina* (H.B. Wood); Delaware Co., on *Hylocichla guttata faxoni*, Oct. 19, and *Agelaius p. phoeniceus*; York Co., on migrating juvenile *Richmondia c. cardinalis*, Sept. 15 (H.M. Martin); Wilkinsburg, Allegheny Co., on *Turdus m. migratorius* (A.D. Kirk); Forest Hill Borough, Pittsburgh, on *Hylocichla mustelina*, said to have carried a Mallophagan which was lost (A.D. Kirk); Beaver, Beaver Co., on *Helmitheros vermivorus*, Aug. 17 (W.E.C. Todd); Blairsville, Indiana Co., on *Colinus v. virginianus*, June 23 (F.C. Bishopp); Norwood, Delaware Co., on *Dolichonyx oryzivorus*, Sept. 14 (C. Liebeck); Moores, Delaware Co., on *Agelaius p. phoeniceus*, Oct. 13 (C. Liebeck). — SOUTH DAKOTA: Brookings, Brookings Co. (J.M. Aldrich). — TENNESSEE: Nashville, Davidson Co., on *Pipilo e. erythrophthalmus*, June 20 (A.R. Laskey). — TEXAS: El Paso, El Paso Co. — UTAH: Hyde Park, Cache Co., on *Colaptes cafer collaris* (G.F. Knowlton and G.S. Stains); Logan, Cache Co. on *Sphyrapicus varius nuchalis* (G.F. Knowlton, G.S. Stains and F.C. Harmston). — VERMONT (recorded by Johnson, 1922, 1925, 1929; Peters, 1933, 1936): Barre, Washington Co., on *Dendrocopos v. villosus*, *Dendrocopos pubescens medianus*, *Melospiza m. melodia*, and *Cyanocitta c. cristata* (Mrs. H.A. Drew); Wells River, Orange Co., on *Melospiza m. melodia*, *Spizella p. passerina*, *Turdus m. migratorius*, Aug. 4, and *Dumetella carolinensis*, Aug. 2 (W. R. Smith); Chittenden, near Rutland, Rutland Co., on *Spizella p. passerina*, Aug. 15 (J. Bequaert); Woodstock, Windsor Co., on *Junco h. hyemalis* (A.P. Morse). — WASHINGTON (STATE) (recorded by Ferris and Cole, 1922; Beer, 1944): Pullman, Whitman Co., on *Zonotrichia leucophrys gambelii*, Sept. 18 (O. Farner and R. Mewaldt); Keyport, Kitsap Co.; Colville, Stevens Co., on *Junco o. oregonus*, Aug. 21 (C.M. Gjullin; A. Walker); Puyallup, Pierce Co. (C.W. Getzen-daner); Conconally, Okanogan Co., on *Dendragapus obscurus richardsoni* (J. Beer); Winthrop, Okanogan Co., on *Dendragapus obscurus richardsoni* (Mrs. Dorothy Schottelius); Twin Buttes, on *Turdus migratorius propinquus*, July 20 (F.C. Bishopp); Kelso, Cowlitz Co., on *Bonasa umbellus togata* (P. Shepardson). — WISCONSIN (recorded by van der Wulp, 1869; Peters, 1936; MacArthur, 1948): Madison, Dane Co., on *Turdus m. migratorius*, Aug. 8 (J. Beer), and on *Zonotrichia albicollis*, Oct. 12 (P. Hickey and W.J. Woodman); Cedar Grove, Sheboygan Co., on *Falco c. columbarius*, Oct. 10, and *Zonotrichia albicollis*, Oct. 5 (L. Diederich);

Milwaukee, Milwaukee Co., on *Zonotrichia albicollis* (A.L. Throne); Milwaukee Co., on *Richmondia c. cardinalis*, Sept. 15, and on *Zonotrichia albicollis*, Sept. 28 (P.W. Hoffman); Lost Lake, Eagle River, Vilas Co., on *Melospiza g. georgiana*, Aug. (A.L. Throne); Wausau, Marathon Co., on *Colaptes cafer collaris*, Sept. 27 (H.W. Levi); Door Co., July 29 (J.H. Roberts); going north toward Peshtigo, Oronto Co., alighting on Man, without attempting to bite, 45° N., June 26 (D.W. Paxson). — WYOMING: Two-Ocean Lake Road, Teton Co., on *Zonotrichia leucophrys gambelii* (N.A. Meinkoth); Jackson Hole Wildlife Park, Teton Co., on *Bonasa umbellus umbelloides* (N.A. Meinkoth).

MEXICO (recorded by Rondani?, 1878; de Buen, 1950):³¹ Mexico City, on "goni6n chico" (possibly *Carpodacus m. mexicanus*) (Esc. N.C.Biol.); Cerro Tancitaro, Munic. Tancitaro, State of Michoacan, 7800 ft., on *Turdus migratorius* subsp. (R. Traub); Patzcuaro, State of Michoacan, on *Catharus o. occidentalis* (P.S. Martin); Temamatla, 2200 m., 35 kilom. S.E. of Mexico City, State of Mexico, 1 ♀ on *Carpodacus m. mexicanus*, July 30 (Mrs. Ana Maríade Buen de Biagi).

O. fringillina is ubiquitous throughout the Holarctic Realm, a northerly type of distribution unique among the Hippoboscidae (Part I, pp. 241-243). It is the bird-fly extending farthest north during the summer (to 68° N. in America and 70° N. in Europe). Moreover, it is confined to the cool temperate areas, as shown below, and strays only exceptionally to subtropical territory. Its present wide range is evidently ancient and wholly natural.

Elizabeth M. Boyd (1951) suggested that probably the starling, *Sturnus vulgaris*, and the English or house sparrow, *Passer domesticus*, were responsible for the introduction of *O. fringillina* into North America. The available evidence contradicts this view. The fly has a great variety of American hosts, having been taken in North America on 107 species (and 26 more subspecies) of native birds, from which I have now 358 verified records. By contrast, there are only 6 records from 4 introduced birds (*Phasianus*, *Acridotheres*, *Passer*, and *Sturnus*). The scarcity of *fringillina* on the European starling, on both sides of the Atlantic, in spite of the prevalence of this bird, marks it as an accidental host. Miss Boyd

³¹ Rondani's supposed "*avicularia*" from Mexico may have been an *Ornithoctona*; van der Wulp's (1903) supposed *Ornithomyia avicularia* from Río Sucio, Costa Rica, seen at the British Museum, is *Ornithoctona fusciventris*.

herself found only one fly by examining 287 starlings during 1944-1946, in New York, Massachusetts, Connecticut, Maryland, Ohio, and Indiana. In addition to a published record from Vancouver (Ferris, 1927), I have seen a third fly from New York. There are only two American records (Ontario and Vancouver) from the English sparrow, which in Europe also is seldom infested. Moreover, historical evidence shows that *O. fringillina* occurred in the United States before the introduction of either starling or English sparrow. Say described his *O. pallida* (a synonym of *fringillina*) in 1823 from a fly taken on the native eastern bluebird. According to May T. Cooke (1928, *U. S. Dept. Agric., Circ. 40*), unsuccessful attempts to introduce the starling were made from 1850 onward, and its permanent establishment in North America dates from about 1869 in Boston and 1890 in New York City. The introduction of the English sparrow occurred from 1850 to 1881 (W.B. Barrows, 1889, *U. S. Dept. Agric. Div. Econ. Ornith. Mammal., Bull. 1*).

The locality records bring out the predilection of *O. fringillina* for a cool temperate climate. Nearly all localities of my list (170 out of 177) are from north of 36° N. Farther south the species is rare and sporadic, as there are no records from Virginia, North Carolina, South Carolina, Georgia, Florida, Alabama, Mississippi, Louisiana, Arkansas and Oklahoma, and only a few from Tennessee (1) Texas (1), New Mexico (2), Arizona (2), and southern California (1 in San Bernardino Co.). The paucity of captures in the southern states cannot be attributed only to the vagaries of collecting, as the small *Ornithoica vicina* is often reported from the same types of hosts in that area. The few southern captures are probably flies carried by migratory hosts arriving from farther north. This might also explain the sporadic occurrences in the Mexican highlands, which, moreover, are faunistically an extension of the Nearctic Region.

In the Old World likewise *O. fringillina* is a fly of the temperate zone. It is the only bird-fly known from Iceland and the boreal parts of Europe and Asia. It is very rare in southern Europe, where it has not been taken south of 40° N.; while in eastern Asia the southmost record is from Fukien (about 27° N.). I know of no reliable capture in the Paleotropics. *Ornithomyia variegata* Bigot, from New Zealand and temperate Australia, appears to be cospecific with *O. fringillina*; in which case the reappearance of the fly in these temperate areas of the southern hemisphere is most probably due to accidental importation by Man.

The distribution of *O. fringillina* contrasts sharply with that of its Old World close relative, *O. avicularia* (Part I, p. 240), which not only avoids the colder temperate regions (being accidental or absent north of 57° N.), but extends over the subtropical and tropical parts of Africa, Asia, the Malay Archipelago and Australia, reaching even Tasmania and New Zealand. The two species overlap over a large zone in the warmer temperate parts of their ranges, where they may be regarded as forming a sympatric pair, sometimes occurring on the same types of hosts or even on the same individual bird (Part I, p. 223).

Known Nearctic Hosts of *O. fringillina* (verified individual records in parentheses). Falconiformes (12 and 2 undetermined hawks): *Accipiter cooperii* (2); *A. striatus velox* (2); *Circus cyaneus hudsonius* (1); *Cathartes aura teter* (1); *Falco c. columbarius* (1); *F. columbarius bendirei* (1); *F. s. sparverius* (3); *Pandion haliaetus carolinensis* (1). Galliformes (26): *Bonasa u. umbellus* (1); *B. umbellus togata* (2); *B. umbellus umbelloides* (4); *B. umbellus yukonensis* (1); *Canachites c. canadensis* (2); *C. franklinii* (3); *Colinus v. virginianus* (1); *Dendragapus o. obscurus* (1); *D. obscurus fuliginosus* (2); *D. obscurus richardsoni* (7); *Lagopus l. lagopus* (1); **Phasianus colchicus* (1). Charadriiformes (3): *Larus delawarensis* (1); *Philohela minor* (2). Strigiformes (8): *Asio wilsonianus* (1); *Bubo v. virginianus* (1); *Glaucidium gnoma californicum* (4); *Otus asio mcallii* (1); *Surnia ulula caparoch* (1). Coraciiformes (1): *Megaceryle a. alcyon* (1). Piciformes (18): *Colaptes auratus luteus* (1); *C. c. cafer* (2); *C. cafer collaris* (2); *Dendrocopos pubescens gairdnerii* (1); *D. pubescens leucurus* (1); *D. pubescens medianus* (2); *D. v. villosus* (1); *D. villosus harrisi* (2); *Picoides arcticus* (2); *Sphyrapicus v. varius* (1); *S. varius nuchalis* (1); *S. varius ruber* (2). Passeriformes (294): **Acridotheres c. cristatellus* (1); *Agelaius p. phoeniceus* (9); *Ammodramus savannarum australis* (1); *Anthus spinoletta rubescens* (1); *Aphelocoma c. californica* (1); *Baeolophus* sp. (1); *B. bicolor* (1); *B. i. inornatus* (1); *Carpodacus mexicanus frontalis* (1); *C. p. purpureus* (4); *C. purpureus californicus* (1); *Compsothlypis americana pusilla* (1); *Corvus brachyrhynchos hesperis* (1); *Cyanocitta c. cristata* (5); *C. stelleri frontalis* (1); *Dendroica a. aestiva* (1); *D. castanea* (1); *D. c. coronata* (2); *D. p. pinus* (1); *D. tigrina* (1); *Dolichonyx oryzivorus* (4); *Dumetella carolinensis* (7); *Euphagus carolinus* (1); *Geothlypis t. trichas* (2); *G. trichas brachidactyla* (4); *Hedymeles ludovicianus* (2); *H. m. melanocephalus* (1); *Helmitheros vermivorus* (1); *Hesperis-*

phona v. vespertina (6); *H. vespertina brooksi* (2); *Hylocichla f. fuscescens* (6); *H. g. guttata* (1); *H. guttata faxoni* (3); *H. mustelina* (3); *H. u. ustulata* (1); *H. ustulata swainsoni* (2); *Icteria virens longicauda* (1); *Icterus galbula* (3); *Junco h. hyemalis* (9); *Junco mearnsi* (1); *J. o. oreganus* (2); *J. oreganus shufeldti* (1); *Lanius ludovicianus excubitorides* (1); *Loxia curvirostra bendirei* (2); *L. curvirostra pusilla* (1); *Melospiza g. georgiana* (4); *M. l. lincolni* (5); *M. lincolni gracilis* (1); *M. m. melodia* (25); *M. melodia gouldi* (2); *M. melodia morphna* (2); *Mniotilta varia* (1); *Molothrus a. ater* (12); *M. ater artemisiae* (1); *Myadestes townsendi* (2); **Passer d. domesticus* (2); *Passerculus sandwichensis savanna* (4); *Passerella iliaca* subsp. (1); *Penthestes* sp. (1); *P. a. atricapillus* (2); *P. h. hudsonicus* (2); *P. rufescens barlowi* (1); *Perisoreus c. canadensis* (1); *Pipilo e. erythrophthalmus* (6); *P. fuscus petulans* (2); *P. maculatus falcifer* (4); *Piranga erythromelas* (1); *P. ludoviciana* (2); *Plectrophenax n. nivalis*; *Poocetes g. gramineus* (2); *Quiscalus q. quiscula* (1); *Q. quiscula aeneus* (3); *Richmondia c. cardinalis* (5); *Sayornis s. saya* (1); *Seiurus a. auricapillus* (2); *S. n. noveboracensis*; *Setophaga ruticilla* (1); *Siala s. sialis* (2); *Sitta* sp. (1); *S. c. carolinensis* (2); *Spizella a. arborea* (1); *S. p. pusilla* (2); *S. p. passerina* (15); **Sturnus v. vulgaris* (2); *Thryomanes bewickii spilurus* (1); *Thryothorus l. ludovicianus* (1); *Toxostoma r. rufum* (7); *Troglodytes a. aëdon* (2); *Turdus m. migratorius* (18); *T. migratorius propinquus* (3); *Tyrannus tyrannus* (1); *Vermivora celata lutescens* (1); *V. peregrina* (1); *V. pinus* (1); *V. r. ruficapilla* (2); *Wilsonia citrina* (1); *Zonotrichia albicollis* (19); *Z. coronata* (4); *Z. leucophrys gambelii* (3); *Z. leucophrys nuttalli* (2); *Z. leucophrys pugetensis* (1). A recent record adds to the Passeriformes *Oporornis formosus*, with 3 flies, at Hyattsville, Prince Georges Co., Maryland, Aug. 3, 1954 (Dr. Leslie Teller).

In addition there are 4 records of *O. fringillina* from Mexico, 3 of them from identified Passeriformes: *Catharus o. occidentalis*, *Turdus migratorius* subsp., and *Carpodacus m. mexicanus*.

Bionomics. The following topics are discussed in Part I: effect of macroclimate (pp. 121-122); parasitism of mites (pp. 152-155); phoresy of Mallophaga (pp. 168-171) and Thysanoptera (p. 174); sex ratio (p. 178); mating (p. 183); larviposition (pp. 191-193); straggling (p. 217); interspecific competition (pp. 223-224); frequency and density of infestation (pp. 229-231); seasonal fluctuations (pp. 241-243); acquired breeding hosts (p. 245); and host specificity (pp. 325-327).

O. fringillina, a polyxenous parasite with little host specificity, breeds successfully on a variety of taxonomically unrelated birds. The Nearctic host list now comprises 107 native species (and 26 more subspecies), in 7 orders; but only the Passeriformes (80 species, with 289 or 80 per cent of the 358 verified records), Galliformes (6 species, with 25 or 7 per cent of the records), and Pici-formes (6 species, with 18 or 5 per cent of the records) contain unquestioned breeding hosts. Certain Falconiformes (7 species, with 14 or 4 per cent of the records) possibly also serve as such in America, as they do in Europe; although birds of prey sometimes acquire flies temporarily from their prey (Part I, p. 216). The fly occurs only as an accidental stray on Charadriiformes (3 records from 2 species), Strigiformes (8 records from 5 species) and Coraciiformes (1 record). *O. fringillina* seems to be much rarer on Galliformes in America than in northern Europe, possibly owing to the successful competition of the larger *Lynchia americana*; but the paucity of records of *Ornithomyia* on American game birds may be due in part to its being often overlooked because of its small size, the few flies per bird, or the swiftness with which it leaves the dead host.

In North America *O. fringillina* sometimes competes with *Ornithoica vicina* on Passeriformes, as discussed before. In the Palearctic Region competition between the closely related *O. fringillina* and *O. avicularia* is presumably keener, as both inhabit in part the same geographical area and often breed on similar hosts (Part I, p. 327). There are now reliable records of *O. avicularia* for 52 species of Palearctic birds in 10 orders; but only Passeriformes (23 species) and Falconiformes (7 species) seem to be true breeding hosts. Fifteen of the 23 Passeriformes and 4 of the 7 Falconiformes have yielded both *avicularia* and *fringillina*; but mixed infestations on the same individual bird are rare (Part I, pp. 223-224).

It is fairly evident that, among the Passeriformes, certain species are favored and others only casual hosts of *O. fringillina*. Of 289 verified native Nearctic records, two-thirds are from members of the 12 genera *Melospiza* (39), *Zonotrichia* (29), *Turdus* (21), *Spizella* (18), *Hylocichla* (16), *Molothrus* (13), *Junco* (13), *Pipilo* (12), *Agelaius* (9), *Hesperiphona* (8), *Dumetella* (7), and *Toxostoma* (7). Moreover, the 80 species from which the fly is known are less than one-third of the Nearctic passerine fauna, of some 300 truly native species. The absence or scarcity of the fly on many passerines cannot be due entirely to insufficient collecting

or to the methods used in obtaining the records, even though the host list will be extended by future observations.

As *O. fringillina* is restricted to cool temperate areas, its yearly life cycle and seasonal fluctuations are of much interest. In Europe the fly seems to overwinter mainly, if not wholly, as puparia, most adults dying off in early winter, regardless of whether the host remains as a winter resident or migrates to warmer quarters; at any rate, flies are found on birds only from early April to mid-November. In North America conditions seem to vary. In the northeastern United States the fly occurs on birds from early July to early November (in Massachusetts from July 3 to November 6); but in the Pacific Coast states, where winters are noticeably milder at the same latitude, it has been taken on birds from March 15 to December 26 and possibly remains on certain birds the year round; and in the Far North, the few records are all from the summer (mid-June to mid-September in Alaska; late July in Yukon; late September in Labrador).

It is as yet uncertain whether *O. fringillina* has one or two generations a year. Ash (1953, p. 207) bred 4 viable puparia obtained from wild gravid flies, in Sweden (3 flies on September 2 and 9) and England (1 fly on July 20), adults emerging the next spring (March 29 to May 28) respectively after 260, 252, 227 and 207 days (average, 237 days). He concluded that there is only one generation a year. As his puparia were deposited in summer, they could be expected to overwinter and produce the flies which infest birds in spring. It remains possible, therefore, that an earlier adult generation might emerge from puparia produced during April and May, which flies could be the chief producers of the later (second) brood of overwintering puparia. Ash (1950, p. 86, as *O. lagopodis*) also reported some 60 flies from a brood in the nest of a merlin, *Falco columbarius aesalon*, in England, July 7, the heaviest infestation on record for *O. fringillina*. The fly is often more abundant on nestlings and fledglings than on adult birds, presumably because the young are unable to get rid of the flies, while the parents do not attempt to remove them. It is difficult to see how heavy nest infestations could be derived only from overwintering puparia, which are never found in large numbers in the nests. More probably they are the offspring produced in spring and early summer when the fly's reproductive activity increases during the brooding season of the hosts, in response to the better opportunities for feeding and pupal incubation. After the fly population is built up in early summer, winter puparia are pro-

duced at a slower rate and the number of flies decreases on the juvenile and adult birds. The available data are inadequate for a study of the seasonal fluctuations of *O. fringillina* in North America, where almost no observations have been made on the larviposition of this fly. Spencer (1938, p. 43) reported finding on a long-eared owl, *Asio wilsonianus*, in British Columbia, in February, a fly dragging its empty puparium; but this does not actually prove that the puparium had been deposited in the feathers of the bird.

The puparium of *O. fringillina* was described or figured in Europe by A.E. Shipley (1909, p. 322; Pl. 44, fig. 25; as *O. lagopodis*) and P. Johnsen (1948, p. 290, figs. 5 and 7); in America by R. Elliott and J. Dearness (1899, p. 60, fig. 34; as *Ornithomyia* sp.) and C.M. Herman (1945, p. 19, fig. 11B; as *O. anchineuria*). The following description is based mainly on a mature puparium obtained from a fly in Massachusetts. It is very broadly oval or sub-circular seen from above (Fig. 28E), 2.8 to 3 mm. long and 2.2 to 2.6 mm. in greatest width (slightly before mid-length), broadly arched at both ends and scarcely narrower behind. In profile it is very lightly depressed, about 1.8 mm. thick, equally convex dorsally and ventrally, with the side edges obtusely rounded. At the posterior end the two peripneustic lobes (Fig. 28C) form one elliptical, slightly raised cap, with wavy, hexagonal contour and a wide, shallow, apical pit; two circular surface structures, placed one on each side in this pit, I regard as the scars of the stigmata of an earlier larval stage, corresponding to the "buttons" of the third stage larva of the Muscoidea; each side half of the cap is divided by depressions into three wedge-shaped raised areas or low ridges, somewhat wider than the depressions, radiating from the apical pit; each ridge bears from 12 to 15 small tubercles corresponding to spiracular pores, placed in a single file which is almost straight near the pit and then curves broadly and regularly at the outer end in the shape of a question-mark; on the ridges, the surface is nearly smooth or with a few wrinkles, but in the intervening depressions it bears a network of engraved lines similar to those found elsewhere on the body, but stronger and more crowded. The integument of the body appears shiny and nearly smooth under a hand-lens; but a high magnification discloses an irregular, polygonal network of fine engraved lines like that of the surface of leather. The larval segmentation is barely indicated here and there by a few superficial, incomplete rows of confluent punctures laterally (but not over the side edges); I can find no trace of similar longitudinal side lines of punctures. At the anterior end, the semi-

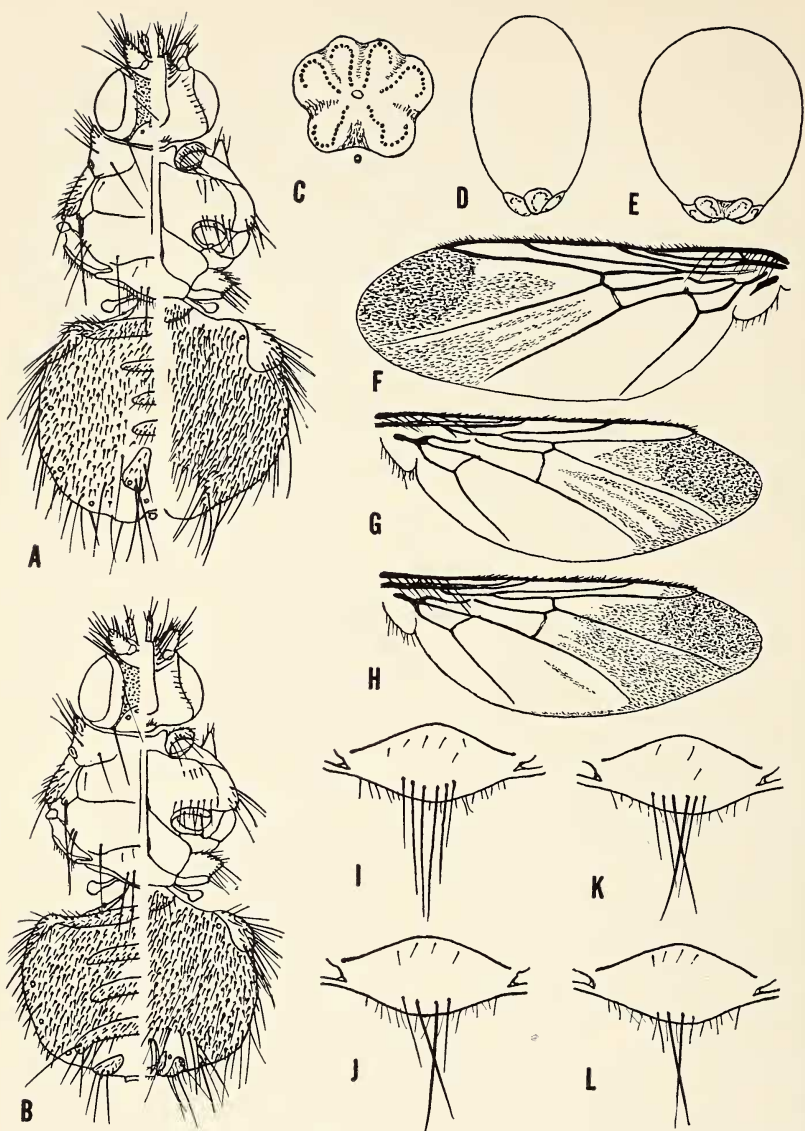


Fig. 28. *Ornithomyia fringillina* Curtis. **A-B**, body in dorsal and ventral view: **A**, ♀, East Westmoreland, on *Melospiza m. melodia*; **B**, ♂, Berkeley, on *Zonotrichia coronata*. **C-E**, puparium: **C**, peripneustic lobes; **D**, puparium in side view; **E**, same from above. **F-H**, wings showing variation in extent of microtrichia; **F**, Curtis' ♀ type (left wing); **G**, ♀, Shorewood near Milwaukee, on *Zonotrichia albicollis*; **H**, ♀, near Peshtigo, Wis. **I-L**, scutellum showing variable number of preapical bristles: **I**, ♀ type of *O. lagopodis* Sharp, Caithness, on *Lagopus scoticus*; **J**, ♀, Newfoundland, on *Hylocichla ustulata swainsoni*; **K**, ♀, Wasau, on *Colaptes cafer collaris*; **L**, ♀, Shorewood near Milwaukee, on *Zonotrichia albicollis*.

circular top seam, along which the puparium splits when the imago emerges, is visible as a slight raised line; but only traces of the circular seam are present at both ends of the semicircular seam.

To the 42 cases of phoresy of Mallophaga mentioned for *O. fringillina* in Part I, the following may be added. Of 2 flies taken on *Pipilo fuscus petulans* by O. E. Sousa at Berkeley, California, one female carried one louse.

Affinities. *O. fringillina* and *O. avicularia* are so closely related that until recently they were commonly lumped or confused. The characters used in my key, although few and of relatively minor importance, separate them clearly. These two flies seem to be what has been variously called dual, vicarious, substitute, representative or sympatric species. The lack of doubtful specimens is particularly conclusive in Europe, where both species are equally common in certain localities, often parasitizing the same birds and sometimes occurring together on an individual host. If they interbred in nature, connecting hybrids would be observed now and then, which is not the case. Moreover, as pointed out by P. Johnsen (1948, p. 290), the puparia offer additional specific characters which remove any doubts that might remain. As compared with *O. fringillina*, the puparium of *O. avicularia* is larger, 3.2 to 3.8 mm. long and 2.8 to 3 mm. in greatest width, more oval from above, and relatively narrower behind; the polypneustic lobes have essentially the structure described for *fringillina*, but each of the radiating ridges bears 15 to 25 spiracular pores grouped radially or placed more or less in two irregular lines; the larval segmentation is fairly well indicated by 10 transverse lines of close set, large punctures, most of the lines broadly interrupted in the middle dorsally and ventrally and all of them lacking on the side edges; and two longitudinal, complete or incomplete lines of similar punctures run on each side a short distance from the edge. The specific distinctness of *fringillina* and *avicularia* may be regarded as well established and is corroborated by their different distribution and ecology.

The two characters separating *O. fringillina* and *O. avicularia* in my key vary within narrow extremes and there is scarcely any overlapping. The wing of *O. avicularia* is 6 to 7.5 mm. long (average, 6.5 mm.); that of *O. fringillina*, 4.5 to 5.5 mm. (average, 4.8 mm.). As is often the case in ectoparasites, dwarfs sometimes occur in both. A male *fringillina*, taken on a brown towhee, *Pipilo fuscus falcifer*, at Berkeley, California, was only 3 mm. in total length (preserved in spirit), with the wing 4 mm. long; whereas other males from the same host in that locality, were nearly 4 mm.

long, with a wing of 5.4 mm. In the European *O. avicularia* seen, the number of preäpical bristles on the scutellum varies from 6 to 10, but most flies have 8 in 4 pairs. In a representative sample of 24 flies, from southern Germany, 1 had 6, 3 had 7, 16 had 8, 1 had 9, and 3 had 10 bristles. The majority of *O. fringillina*, both in Europe and in North America, have 4 scutellar bristles in 2 pairs; but the median pair is always stronger and the outer one is weak, often hair-like; one must be careful not to overlook bristles that are broken, but can be traced by the minute, pit-like sockets. Flies with only 3 bristles (one of the outer pair missing) are not very rare; those with 5 or 6 bristles are exceptional; and I have seen one fly, from Babylon, New York, with only 2 bristles.

Additional structural differences, which I used at one time (Bequaert and Leclercq, 1947), are too subtle or too variable for practical purposes. Usually the interocular face of *fringillina* is not or barely longer than wide at postvertex, with the inner eye margins distinctly diverging upward; whereas in *avicularia* it is often somewhat longer than wide at postvertex, with the eye margins only slightly diverging. Measurements of a series of flies show that even the average difference is too slight to be trusted and that both species are sometimes almost identical in this respect. There is, moreover, no appreciable sexual difference in the width of the face. The difference in general shape or contour of the head is even less reliable than that of the face.

The different size of the ocelli is clear enough when the two species are compared, but difficult to appraise when only one is on hand. In *O. avicularia*, the anterior ocellus is about as wide as two-thirds of its distance from the posterior pair and usually placed well below a line drawn through the upper eye margins. In *O. fringillina*, the ocelli are smaller and therefore farther apart, the anterior ocellus being only as wide as one-third to one-half of its distance from the posterior pair and usually placed on or barely below a line drawn through the upper eye margins.

Minor differences in the venation of the wing are favored by many dipterists, because they are so easily seen. In *Ornithomyia* they vary much within the same species. In particular, the course of the longitudinal veins, the position and length of the cross-veins and the relative length of the basal and anal cells should not be given undue importance. Owing to the wide range of variation, obvious differences appear when a few specimens are compared; but they break down when large series are studied, as it is impossible to correlate them consistently with other, more reliable char-

acters. Possibly a comparative statistical study of a few hundred specimens may reveal reliable average differences in the venation of *O. avicularia* and *O. fringillina*. Smart (in Edwards, Oldroyd and Smart, 1939, p. 119) states that in *avicularia* the anterior basal ["medio-cubital"] cross-vein is 4 times the length of the anterior ["radio-median"] cross-vein and the anal vein shorter; whereas in *fringillina* the anterior basal cross-vein is only twice the length of the anterior cross-vein and the anal vein longer. This is no doubt correct in many cases; but some *avicularia* and *fringillina* show no appreciable difference in this respect, the anterior basal cross-vein being sometimes about 3 times the length of the anterior cross-vein. The comparative length of the two terminal sections of the costa has also been used as a specific character. In most *fringillina*, the two sections, set off by the 2nd longitudinal vein, are about equal or the last section is slightly shorter; but in some, the penultimate section is nearly $1\frac{1}{2}$ times the length of the last. In *avicularia*, the penultimate section is from $1\frac{1}{2}$ times to almost twice as long as the last; again this varies, although I have not seen an *avicularia* with both sections nearly equal. In many *fringillina*, the anal cell is relatively shorter and wider than in most *avicularia*; but the difference is sometimes imperceptible. The distance between the anterior and the anterior basal cross-veins on the 4th longitudinal varies also and some specimens of either species are identical in this respect.

In both *avicularia* and *fringillina*, microtrichia cover only a small area of the wing membrane. They are restricted as a rule to the 1st and 2nd posterior cells; exceptionally a few hairs occur in the tip of the submarginal cell or form a narrow streak in the apical portion of the 3rd posterior cell; the 1st and 2nd posterior cells usually have some bare streaks, but these vary greatly (Figs. 28F-H). Three flies from Alaska grouse, at Fairbanks, Alaska, are more extensively hairy on the wings than any other seen: there are no bare streaks in the 1st and 2nd posterior cells, which are bare only at the extreme base; one of these flies has an additional narrow streak of hairs in the 3rd posterior cell.

Séguy (1936, pp. 105-106) used for specific distinction the so-called jugular bristles ("soies jugulaires") on the antero-ventral portion of the head. These correspond to the vibrissae of the Muscoidea, being placed on the facial ridges at the upper sides of the cavity containing the rostrum membrane and mouth-parts. Owing to the flattening of the head, the facial ridges and their vibrissae have shifted to a ventral position between the antennal pits and the buccal cavity (Fig. 3C). According to Séguy, *O. avi-*

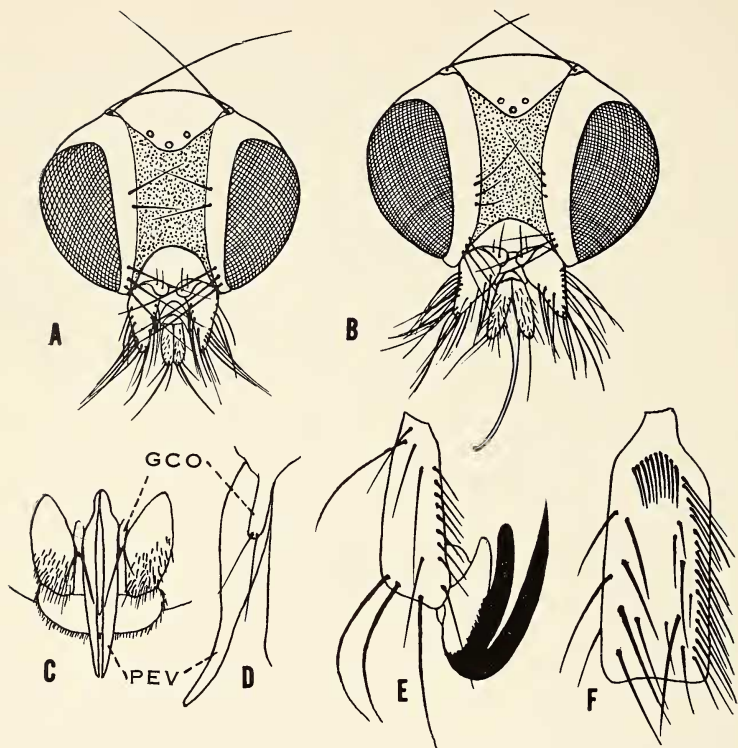


Fig. 29. *Ornithomyia fringillina* Curtis. A-B, head: A, Curtis' ♀ type; B, ♂, Goat Mountain, on *Dendragapus obscurus richardsoni*. C-D, ♂ terminalia, Berkeley, on *Zonotrichia coronata*: C, from below; D, in side view; GCO, gonocoxite; PEV, penis valve. E, distitarsus and claw of hind leg, ♀, Oak Bluffs, on *Spizella p. passerina*. F, basitarsus of hind leg from beneath, ♂, Harlan Gulch, on *Dendragapus obscurus richardsoni*.

cularia has 8 to 12 vibrissae, while *O. fringillina* (= *O. chloropus*) has 6 strong vibrissae or exceptionally 8. A study of many specimens has convinced me that the difference is due mainly to the fact that in *avicularia* the vibrissae are stronger, so that some that are only short setae in *fringillina* now appear as long bristles.

The abdomen of *fringillina* bears the same median dorsal sclerites as that of *avicularia*, and the slight differences in size and shape do not help specific identification. In the males, the first two sclerites are longer and wider in *fringillina* than in *avicularia*, so that they are more like the third sclerite. In the female, all three sclerites are wider and longer in *fringillina* than in *avicularia* and

about the same size or the third a little larger. (In Ferris and Cole, 1922, p. 199, fig. 15 of a female *fringillina* shows the first sclerite partly concealed beneath the basal plate, as pointed out by the authors.)

The penis valves or parameres of the male terminalia are so similar that only a direct comparison shows the difference. In *fringillina* they are slender throughout seen from below, and slightly and very gradually widened basad in side view; in *avicularia* they are broader basally and more abruptly widened at the apical third. A somewhat similar difference in the parameres has been claimed between *fringillina* and so-called *lagopodis*; but I suspect that the comparison was usually made with specimens of *O. avicularia* misidentified as *fringillina*, a confusion often made in the past.³² The small finger-shaped gonocoxites (Figs. 29C-D) are slender, weakly sclerotized and with 2 short bristles as the tip.

I regard color characters, with few exceptions, as unreliable in Hippoboscidae (Part I, pp. 57-60), and this is particularly true for *Ornithomyia*. As there are often fairly definite color differences between certain specimens of different species, it is difficult to be convinced that these differences are not of specific value. But, if many specimens are compared, it soon becomes impossible to find a consistent color difference between *avicularia* and *fringillina*, both species varying from light russet to mahogany-brown, with faint or more pronounced darker areas. The color of the palpi in particular, used by Smart (1939), is often exactly the same in both species. Smart also separates *lagopodis* and *fringillina*, which I regard as conspecific, on the basis of color; to *fringillina* he refers the specimens with the head and thorax uniformly pale; while those with dark markings on the under side of head and thorax he calls *lagopodis*. It is, of course, possible to arrange most of the small *Ornithomyia*, both in Europe and North America, in two groups according to this character; but there remain transitional specimens which must be placed arbitrarily. Moreover, the color differences are not correlated with any other character, certainly not with any difference in size or in extent of the microtrichia in the wing, as Smart implies (*fringillina* with a wing span of 10 mm. and less pubescent wings; *lagopodis* with a wing span of 12 mm.

³² Although Smart (1939, p. 119) bases his key on characters which I regard as unreliable, in the text he points out correctly that *avicularia* is larger (with a wing span of nearly 15 mm.) than *fringillina* or "*lagopodis*" (with a wing span of 10 to 12 mm.).

and more pubescent wings). Most North American *fringillina* are light reddish-brown, yet often as large and as extensively hairy on the wings as the dark-colored Scottish grouse-flies. Some American specimens also are dark mahogany-brown; one such fly, with the wing 5.5 mm. long and 4 præapical scutellar bristles, came from *Zonotrichia leucophrys gambelii* in the State of Washington, where the summer is usually cool and damp. It might be advisable to investigate whether the darker color of the *fringillina* found on grouse in Scotland is due to the macroclimate, to an ecological peculiarity of the host, or to some other factor.

According to Smart (1939), freshly-caught *avicularia* and *fringillina* have a greenish tinge in their body coloration never found in *lagopodis*. This dull, grass-green color of certain hippoboscids, probably produced under suitable conditions by all species of *Ornithomyia*, is caused by a green pigment in the haemolymph (Part I, pp. 58-60). It is absent in the newly-emerged fly and develops some time after feeding. It disintegrates rapidly after death if the insect is preserved in spirit and more gradually if it is kept dry, traces remaining longer in the legs and in the main veins of the wings than elsewhere. It should be noted that specimens now found pinned in collections may have been at first preserved in spirit. The green color may also be hidden in the live fly by the darkening of the integument, possibly explaining why it was not noticed in the so-called *lagopodis*.

Original description of *O. fringillina*: "Ochreous, inclining to bright green; hairs black; maxillae, eyes, a spot on the base of each antenna, and another where the ocelli are placed, piceous; head and thorax shining ochreous, faintly variegated with brown, leaving a pale line down the back; abdomen dull green, pilose; wings iridescent, slightly smoky, with a darker large oval spot at the apex; nervures black; legs verdigris-green; tibiae with a black streak outside; claws and upper side of terminal joint of hinder tarsi black." Curtis drew up this description from at least three specimens, two of which appear to be lost. The third, a ♀ now at the Australian National Museum in Melbourne, may therefore be designated as the lectotype. Mr. Gordon B. Thompson (1936) published on it the following notes, based on my own examination of the specimen: "The type is a well-preserved female, without indication of locality or host. It agrees in every respect with the common, smaller species of *Ornithomyia*, described by Bergroth as *O. chloropus* and by Sharp as *O. lagopodis*. The head is distinctly wider than high. The vertex [postvertex] is moderately long, so that the anterior ocellus lies slightly below a line drawn through the upper orbits. Inner orbital bristles few, in two widely separated groups (2 placed about the middle, 3 near the lower edge); gula (ventrally) with setae only on the low, somewhat converging ridges separating the infrabuccal membrane from the postgenae; no postorbital setae. Ocelli small. Frons [interocular face] nearly twice the width of an eye. Fronto-clypeus [frons] with a shallow median pit-like depression near the upper margin. Scutellum fringed with short, sparse hairs along the extreme hind margin and with 2 pairs of præapical bristles, of which the inner pair is much the longer; disk otherwise

bare. Humeral angles short and broad, barely reaching beyond the upper margins of the eyes. Wing short, 5 mm. long; apical section of costa about two-thirds of the length of the penultimate section; second basal cell (*M*) short and of normal width, closed by an anterior basal cross-vein (*m-cu*) which is about twice the length of its distance from the anterior cross-vein (*r-m*); anal cell (*1st An*) much less than half the length of the second basal cell. Length (from tip of palpi to tip of abdomen), in dry condition, 3.6 mm." Head and wing of this type specimen are drawn in Figs. 29*A* and 28*F*. Continental European authors have used the name *O. fringillina* for the long-headed species of barn swallows, *O. biloba* Dufour, clearly an erroneous identification, as the barn swallow fly has never been taken in the British Isles.

Original description of *O. pallida*: "Pale; intermediate cellule of the wing extending nearly to the tip of the outer cellule. Eyes blackish-chestnut; antennae chestnut, tip white; labrum bifurcated, white; hypostoma whitish; front yellow-white, a brown lunule above the hypostoma and spot on the vertex; throat and cheeks white; thorax varied with pale-yellowish and pale honey-yellow, impressed cruciform lines distinct; scutell pale honey-yellow, edged with pale-yellow; costal nervures dark-brown, at base, and those of the disk brown, the transverse nervure of the intermediate cellule is in contact with that of the preceding cellule; pectus and feet white, tibia with a brown line, tarsi tinged with green; nails black; abdomen yellowish-white. Length less than $\frac{1}{2}$ inch [5 mm.]." Say's type is lost, but there can be little doubt that he described the common North American *Ornithomyia*.

O. anchineuria Speiser, being merely a change of name, has no type properly speaking. It is doubtful that Speiser saw a specimen at the time he proposed the new name, the character of the "basal cells nearly equally long," which he mentions, being seemingly taken from Say's description.

Original description of *O. chloropus* (German text translated): "Fusca, angulis anticis prothoracis et pectore pallide testaceis, capite subtus, maculis duabus basalibus elongato-triangularibus exceptis, dilute virescente, pedibus aeruginosis, alis leviter umbratis, venis nigris, vena longitudinali quarta ante medium cellulae basalis posterioris, anguste et vena transversa posteriore medio late albo-interruptis, vena longitudinali prima duplicata longius ante venam transversam anteriorem in costam exeunte, apice venae longitudinalis secundae ab apice primae ac tertiae aequae longe distante, cellula basali posteriore anteriore paullo brevior et cellula anali duplo et dimidio longiore. Long. corp. 4-4.5 mm., alae 5 mm. Brown, fairly shiny, with black setae. Head circular, brown above, paler and more shiny at base and on orbits, ocellar spot [post-vertex] distinct, but ocelli flat and inconspicuous; a seta at the base of the antennae, in the middle of the orbits and some distance behind the posterior angle of the eye; the semi-lunate plate above the antennae [lunula] slightly depressed, somewhat angular posteriorly; antennae moderately wide, with long setae, curved and claw-shaped, convex above, concave below, yellow, blackish at base and tip; proboscis black, the single middle piece not extending beyond the lateral valves [palpi], which are setulose at tip; head pale green below, on each side with an elongate, triangular, basal brown spot, which extends beyond mid-length where it ends in a point; anteriorly one or two longer setae on each side before the oral margin; medially, between base of antennae and proboscis, several shorter setae at oral margin, so close as to simulate a palp-like organ. Thorax above with a fine impressed longitudinal line, laterally with some long setae, brown, the anterior angles rather extensively yellowish but with a brown spot, the sides also paler, the dorsum arched before the scutellum. Scutellum about twice as broad as long, brown, finely cross-wrinkled, setose at apex. Sternum pale yellowish, laterally with some weak setae before mid coxae. Wings slightly infusate, extending for over half the length beyond tip of abdomen; veins of anterior half thick and black as usual, those of posterior half pale and much thinner; costa sparsely setose near base; 1st

longitudinal vein ending in costa rather far basad of anterior cross-vein; tip of 2nd longitudinal midway between that of 1st and 3rd longitudinals; 4th longitudinal with a narrow white ring [bulla] before mid-length of posterior [2nd] basal cell, where it is angularly interrupted and runs close to base of 3rd longitudinal; posterior [anterior basal] cross-vein at least 3 times as long as anterior cross-vein, broadly white [with a bulla] in the middle; posterior [2nd] basal cell a little shorter than anterior [1st] basal cell and $2\frac{1}{2}$ times as long as anal cell. Legs verdigris, tinged with yellowish in spots; femora and tibiae compressed; fore femora much broadened above, with some very long setae on front side of apical half; legs otherwise rather sparsely and uniformly setose; terminal segment of fore tarsi nearly as long as other segments combined; terminal segment of hind tarsi relatively shorter; claws black, but basal accessory tooth ["heel"] pale reddish-yellow, at least apically; main teeth with a small seta on basal upper half. Abdomen a little shorter than thorax, somewhat wider than long, brown, with rounded sides, puffy, greenish-yellow, setulose, the setae longer toward apex, which is deeply notched for the genitalia." Although the sex is not mentioned, the final statement in the description makes it fairly certain that the two cotypes were females. The new species is said to differ from *O. avicularia* in that "the distance between the tips of the 1st and 2nd longitudinal veins equals that between the tips of the 2nd and 3rd; whereas in *avicularia* the former distance is at least twice the latter;" from *O. fringillina* Curt. (*tenella* Schin.) in the "considerably shorter 1st longitudinal vein;" and from *O. metallica* Schin. in the much longer posterior [2nd] basal cell. The description originally given of the venation of *O. ptenoletis* is said to be so confused that a comparison is difficult, although that species, it is claimed, cannot be the same as *O. chloropus*. The comparisons with other species are very vague. The location of the 2 cotypes was not given and they are not now at the Zoological University Museum in Helsingfors. They may have been returned to the collector, V. Pousar. Of 18 *Ornithomyia* taken in Finland and received from Dr. R. Frey, 17 were what I call *fringillina* and only one the large *O. avicularia*. None of these *fringillina* were from Bergroth's type host; but three were from other species of owls, *Asio otus*, *Surnia ulula*, and *Bubo bubo*, showing that, in Northern Europe at any rate, *O. fringillina* is a frequent parasite of nocturnal birds of prey. Some of these specimens had been labelled before *O. chloropus*. European flies received as *O. chloropus*, from other sources, were invariably *fringillina*. Bergroth's description fits that species well. His comparison with a supposed "*fringillina*" was actually with *O. biloba* Dufour (= *O. tenella* Schiner).

Original description of *O. lagopodis*: "Supra nigricans, subtus pallide testacea, pedibus fusco-testaceis; pectore utrinque fusco-nigro-biplagiato. Long. corp. 5 mm.; expans. alarum, $11\frac{1}{2}$ mm., long. alae sing., 5 mm. Smaller than *O. avicularia*, distinguished by its peculiar lurid blackish color, without any trace of green even on the feet or legs; the rostrum is black and the hairs of the body and appendages are shorter than in the better known form; on each side of the thoracic pleuron, between the front and middle legs, there is a very large dark patch extending as far towards the middle as the base of the front coxa, and divided into two parts by an oblique pallid line. The head is considerably smaller and narrower than that of *O. avicularia*, and has beneath a very large area of smoky color on each side. Mr. Collin has pointed out to me that the segments, or abscissae, of the costa afford a good character; the relative lengths of the outer two being in *O. lagopodis* as 9 to 8, and in *O. avicularia* about 12 or $12\frac{1}{2}$ to 8. The bristles on the scutellum are usually more numerous, as well as larger, in *O. avicularia*." Sharp described the species from 26 specimens collected in Scotland, either on grouse or without a host. Several of these are now at the British Museum and two, from Caithness, mounted side by side on a pinned square of cork, are labelled "types." According to Dr. G. B. Fairchild (*in litt.*, 1953), in one of these types both wings are 5 mm. long, while in

the other the left wing is 4.9 mm. and the right, 5.2 mm. Two paratypes, from Caithness, are now at the Museum of Comp. Zool., through the kindness of Dr. H. Oldroyd. In the specimens from Caithness there are usually 3 pairs of preapical scutellar bristles, but the outer pair are very short and weak. I have given my reasons before for regarding *lagopodis* as not separable from *fringillina*.

Ornithomyia parva Macquart

Figs. 30A-E

- Ornithomyia parva* Macquart, 1843, Mém. Soc. R. Sci. Agric. Arts Lille, (for 1842), p. 436 (no sex; no host. "From Brazil or Chile." Presumed 4 cotypes from Bigot Coll., now in the J. E. Collin Coll.) [1843, Dipt. Exot., 2, pt. 3, p. 279]. Walker, 1849, List Dipt. Brit. Mus., 4, p. 1143.
- Ornithomyia remota* Walker, 1849, List Dipt. Brit. Mus., 4, p. 1144 (no sex; no host. "Isle of Trisram [=Tristan] da Cunha." Type ♀ at Brit. Mus.). J. Bequaert, 1951, Agricultura Técnica, Santiago de Chile, 10, pt. 1, (for 1950), p. 7. Crichton, 1951, Ent. Mo. Mag., 87, p. 21 (Tristan da Cunha Group: Nightingale I., on *Nesospiza wilkinsi*; Inaccessible I., on *Nesospiza acunhae*. Gough I., on *Nesospiza jessiae* or *N. goughensis* and *Porphyriornis comeri*. Notes on Walker's type). J. Bequaert, 1954, Res. Norwegian Sci. Exped. Tristan da Cunha 1937-1938, No. 26, p. 45.
- Ornithomyia avicularia* Austen, 1903, Ann. Mag. Nat. Hist., (7), 12, p. 261 (in part: type of *O. remota* Walker only); 1906, Illustr. British Blood-Suck. Flies, p. 64 (in part: Tristan da Cunha). Falcoz, 1930, Encyclop. Entom., Sér. B, Diptera, 5, (for 1929), p. 32 (listed doubtfully from Chile). Not of Linnaeus, 1758.
- ? *Ornithomyia synallaxidis* Lynch-Arribáizaga, 1881, Expedición Río Negro, Informe Oficial, 1, Zool., p. 90 (no sex. Argentina: Río Negro, on "*Synallaxis patagonica*" [*Asthenes patagonica*]. Type presumably lost); 1881, Stettin. Ent. Zeitg., 42, p. 192 (German translation of original description). Berg, 1881, Op. cit., 42, p. 46.
- ? *Ornithoctona* (?) *synallaxidis* Speiser, 1902, Termész. Füzetek, 25, p. 329. Brèthes, 1907, An. Mus. Nac. Buenos Aires, 16, p. 302. Speiser, 1908, Zeitschr. Wiss. Insektenbiol., 4, p. 304.
- Ornithomyia chilensis* E.C. Reed, 1904, Rev. Chilena Hist. Nat., 8, p. 152 (no sex. Chile: Concepción, on "*Diuca grisea*" [*Diuca d. diuca*]. Described from 3 specimens; holotype ♂ and paratype ♀, from Reed Coll., now at California Ac. Sci., San Francisco; present location of 3rd type not definitely known). Not *Ornithomyia chilensis* Macquart, 1843.
- Ornithomyia chilensis* E.P. Reed, 1932, Rev. Chilena Hist. Nat., 35, (for 1931), p. 103 (Chile: Valparaíso, on *Diuca d. diuca*, *Agriornis l. livida*, *Turdus magellanicus*, *Mimus thenca*, and *Glaucidium nanum*; some of the specimens carrying Mallophaga of the genus "*Degeeriella*" [= *Brüelia*] and others with mites, supposedly *Myialges caulotoon*).
- Ornithomyia paricella* Speiser, 1905, Zeitschr. Syst. Hym. Dipt., 5, p. 349 (no sex; new name for *O. chilensis* E.C. Reed, 1904; with new description of 3 specimens in Speiser Coll., from Concepción, Chile, on *Diuca d. diuca* and *Muscisaxicola macloviana mentalis*); 1908, Zeitschr. Wiss. Insektenbiol., 4, p. 304. J. Bequaert, 1933, Rev. Chilena Hist. Nat., 37, p. 162. Stuardo, 1946, Catálogo Dípteros Chile, p. 187.
- Ornithomyia anchineuria* Donoso Barros, 1949, Rev. Médica Chile, 77, p. 404 (Chile: Arica, on *Agriornis l. livida* and biting Man). Not of Speiser, 1905.

Distribution and Specimens Examined. TRISTAN DA CUNHA GROUP (recorded by Walker, 1849, as *O. remota*; Crichton, 1951, as

O. remota): Inaccessible I., 2♂ on *Atlantisia rogersi* (received from Dr. F. Zumpt), 2♀, 3♂ on *Nesospiza acunhae* (G.J. Broekhuysen), 3♀ on *Nesocichla eremita gordonii*, one carrying 2 Mallophaga (Norway Sci. Exp.—Y. Hagen), and 4♀, 6♂ probably on *Nesospiza acunhae* (Norway Sci. Exp.—Y. Hagen); Nightingale I., 1♀ on *Nesospiza wilkinsi* (G.J. Broekhuysen), 1♀, 1♂ on *Nesospiza wilkinsi* (Norway Sci. Exp.—Y. Hagen), and 2♀, 2♂ on *Nesocichla eremita gordonii* (Norway Sci. Exp.—Y. Hagen).

GOUGH ISLAND (recorded by Crichton, 1951): 1♂ on *Nesospiza jessiae* or *N. goughensis* (G.J. Broekhuysen); 2 specimens on *Porphyriornis comeri* (G.H. Wilkins).

ARGENTINA (probably recorded by Lynch Arribálzaga, 1881, as *O. synallaxis*): Valle del Lago Blanco, Chubut (J. Koslowsky); Cafayate, Calchaquí Valleys, 1650 m., Salta, Aug. 17, on *Embernagra platensis olivascens* (K.J. Hayward); Agua Tapada, Distr. Hualfín, Catamarca, on *Caracara p. plancus*, July 19 (S. Pierotti).

CHILE (recorded by E.C. Reed, 1904, as *O. chilensis*; Speiser, 1905, as *O. paricella*; E.P. Reed, 1932, as *O. chilensis*; Donoso Barros, 1949, as *O. anchineuria*): several without precise locality, mostly without hosts, but 1♀ on *Agriornis l. livida*; including holotype ♂ and paratype ♀ of *O. chilensis* Reed; 3 of these specimens carrying Mallophaga; Valparaíso, 1♀, 1♂ on *Diuca d. diuca*, one with a Mallophagan, *Brüelia* sp., attached (E.P. Reed); Tofo, 1♀ (T. Hallinan); Maquehue, Temuco, 38° 47' S., on *Sturnella militaris* (R.M. Middleton), *Agelaius t. thilius*, May 23, *Diuca d. diuca*, June 24, and 3 specimens on *Colaptes p. pitius*, one carrying a Mallophagan; Angol, on *Turdus magellanicus*, Aug. 15, *Cinclodes nigro-fumosus*, April 26, June 27 and July 11, *Diuca d. diuca*, Apr. 2, and *Zonotrichia pileata*, Aug. 10 (D.S. Bullock); Concepción (C. Castillo; P. Herbst); Conceon, near Valparaíso (A. Wetmore); Galvarino, on *Zonotrichia pileata* (E.P. Reed); Llico, 37° 14' S., on *Diuca d. diuca* (E.P. Reed); Baños de Cauquenes (P. Herbst).—In the Bigot Collection, now with Mr. J.E. Collin, 4 flies from Chile, labelled "*O. parva*," are in my opinion the types of Macquart's species of that name.

O. parva is the only louse-fly of the few endemic land birds of the Tristan da Cunha and Gough Islands. The compact Tristan da Cunha Archipelago, of 3 small islands and 2 islets, lies in the South Atlantic (about 37° S. and 12° 30' W.), some 1800 miles W. of South Africa and some 3000 miles E. of Argentina. Gough or Diego Alvarez, 220 miles S. of the Tristan Group, is very small. Walker described *O. remota* from Tristan da Cunha in 1849. No

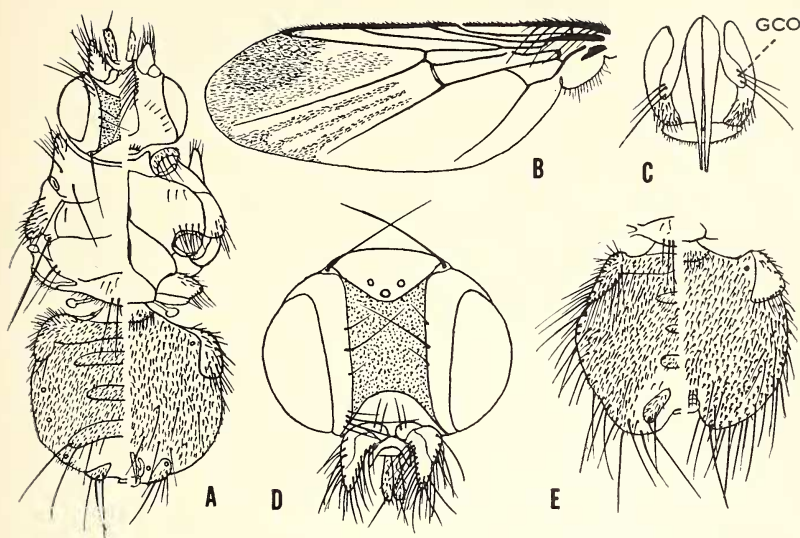


Fig. 30. *Ornithomyia parva* Macquart. A, body in dorsal and ventral view, ♂, Valparaíso. B, wing ♀, Valparaíso. C, ♂ terminalia from below, Nightingale I., on *Nesocichla eremita gordoni*; GCO, gonocoxite. D, head, ♀, Valparaíso. E, abdomen and scutellum in dorsal and ventral view, ♀, Nightingale I., on *Nesocichla eremita gordoni*.

bird-flies were taken there for nearly a century, until 3 recent parties of ornithologists collected several on 2 of the Tristan Islands, but not on the main island, whose land birds are almost extinct; and some also on Gough. I have seen 30 specimens from these islands, taken on 6 hosts, including all 4 land birds now living on the Tristan Group and 2 of the 3 known from Gough. The species of fly is common on various birds in Chile and Argentina and was, I believe, first described by Macquart as *O. parva*, the later *O. remota* Walker and *O. chilensis* E.C. Reed (renamed *O. paricella* by Speiser) being synonyms. As this fly is unknown from the Old World, it must have reached Tristan da Cunha and Gough from South America either with some of the ancestors of their endemic birds or later on birds that strayed accidentally to the islands. The present distribution of *O. parva* possibly supports the current view that the terrestrial birds of the South Atlantic islands are modified South American types and not related to those of Africa.

The known continental records of *O. parva* show that it is peculiar to temperate, extratropical South America. Northward it reaches about 26° S. in the highlands of western Argentina, but not

as far in southeastern Brazil. At any rate, it was not represented in a fairly large series of hippoboscids collected by Fritz Plau-
mann in the State of Sa. Catharina (27° S.) (J. Bequaert, 1943c).
The distribution of *O. parva* is the counterpart of that of *O. fringil-
lina* in temperate North America, both species avoiding areas with
a tropical climate.

Known Hosts of *O. parva* (verified individual records in paren-
theses): Falconiformes (1): *Caracara p. plancus* (1). Gruiformes
(2): *Atlantisia rogersi* (1); *Porphyriornis comeri* (1). Strigi-
formes: *Glaucidium nanum*. Piciformes (1): *Colaptes p. pitius*
(1). Passeriformes (21): *Agelaius t. thilius* (1); *Agriornis l.
livida* (1); (?*Asthenes patagonica*, if *O. synallaxidis* is a synonym
of *O. parva*); *Cinclodes nigro-fumosus* (3); *Diuca d. diuca* (4);
Embernagra platensis olivascens (1); *Mimus thenca*; *Muscisaxicola
macloviana mentalis*; *Nesocichla eremita gordonii* (2); *Nesospiza
acunhae* (2); *N. jessiae* (or *goughensis*) (1); *N. wilkinsi* (2);
Sturnella militaris (1); *Turdus magellanicus* (1); *Zonotrichia
pileata* (2).

This host list will no doubt be greatly extended by future col-
lecting, as *O. parva* is probably the most common bird-fly in tem-
perate South America. The species agrees with the Holarctic *O.
fringillina* in favoring certain Passeriformes for breeding purposes,
while showing otherwise no very strict host preference. The few
records on two flightless rails in Tristan da Cunha (*Atlantisia*)
and Gough (*Porphyriornis*), though of interest, are inadequate to
decide whether these birds are efficient breeding hosts; perhaps the
fly only strays to them occasionally from the *Nesospiza* and *Neso-
cichla*, with which they are closely associated in the same environ-
ment.

O. parva shares with the two common *Ornithomyia* of the North-
ern Hemisphere the frequency with which it transports Mallophaga.
As noted in Part I (pp. 171-172), of some 50 flies seen, 6, from 3
species of birds, carried such lice (1 from the Tristan da Cunha
Group and 5 from Chile). In addition to the flies mentioned in
Part I (p. 155), I have seen several others, from Chile, infested
with mites.

A puparium of *O. parva*, found by Y. Hagen in the plumage of
a juvenile female *Nesocichla eremita gordonii*, on Inaccessible I.,
Jan. 20, 1938, is probably premature, as it is light-brown. It is
shaped like that of *O. fringillina*, 2.6 mm. long, 2.2 mm. wide and
1.5 mm. thick. As in that species, the spiracular pores of the

peripneustic lobes are arranged in a curve shaped like a question-mark on each ridge.

Affinities. In the genus *Ornithomyia*, *O. parva* belongs to the *avicularia* group and is most closely related to *O. fringillina*. From the latter it differs in the decidedly wider interocular face, which is much alike in both sexes; the inner orbits are also relatively wider. The ocelli are rather large, the anterior ocellus nearly as wide as its distance from the posterior ocelli. Dull green pigment in the haemolymph was observed in several specimens. The extent of mitrotrichia in the wing (Fig. 30B) is as in *fringillina*; a very narrow streak of hairs is sometimes present in the 3rd posterior cell. In the male terminalia (Fig. 30C), the gonocoxites are wider than in *fringillina*, more lobe-like, and bear a short row of 3 bristles, which are longer than in *fringillina*. I can see no tangible difference in the shape of the penis valves.

Original description of *O. parva* (French text translated): "Pieea. Capite testaceo. Pedibus flavidis. Long 2 l. [2 French lines = 4.5 mm.] Pitch-black. Head dark testaceous. Sides of head and occipital spot shiny black. Legs greenish-yellow; femora brownish above, hirsute on upper side only. Legs somewhat yellowish; 2nd [anterior basal] cross-vein very close to the 1st [anterior]." The specimens, collected by Gaudichaud in "either Brazil or Chile," were said to be at the Paris Museum. So far as could be traced, there is no specimen now at the Paris Museum labelled *Ornithomyia parva*; but there is a fly collected by Gaudichaud in 1833 at Valparaiso, Chile, belonging to the species described by Walker (1849) as *Ornithomyia remota*.³³ It is not impossible that this insect was seen by Macquart, even though he was uncertain about the locality. It might even be one of the types of his *O. parva*, although the matter must remain in doubt. In the Bigot Collection, now part of the J. E. Collin Collection, 5 specimens now stand under the label "*Ornithomyia parva*." One of these, from "New Grenada," was examined by Speiser (1902), who recognized it correctly as a species of *Ornithoctona*. It is actually *Ornithoctona fusciventris* (Wiedemann) and is discussed more fully under that species. I do not regard it as a possible type of Macquart's *parva*, because it is too large and does not otherwise agree with the description, notably in having the "second cross-vein" rather far from the "first," as usual in *Ornithoctona*, certainly not very close to it, the condition more common in *Ornithomyia*. The remaining 4 flies, labelled "Chile," are smaller and agree well with Macquart's description. They are *Ornithomyia* in the modern sense of the genus and conspecific with Walker's *O. remota* and E. C. Reed's *O. chilensis* (= *O. paricella* Speiser). The antennal appendages are slender, not leaf-like; the anterior ocellus is placed slightly below the level of the upper eye margins and the wings are about 6 mm. long. As no other species of *Ornithomyia* is known at present from Chile, I have reached the conclusion that these 4 specimens are at least part of the original type lot of *O. parva*, which were not returned to the Paris Museum and later found their way to Bigot's collection; if so, *O. parva* is the earliest valid name for the *Ornithomyia* of temperate South America.

³³ The specimen now bears an old label with the name "*Ornithomyia platycera*"; but it is not the African species of that name, which is an *Ornithoctona*.

Original description of *O. remota*: "Fulva, scutello sulcis transversis vitato, pedibus fulvis, alis subfuscis. Body pale tawny: head and chest smooth, shining: eyes pitchy; facets rather large: mouth pitchy: scutcheon traversed by a row of slight furrows, widening from the fore border to the hind border, which is beset with a few stout black bristles: abdomen mostly dull, clothed with short black hairs, its tip beset with long black bristles; legs tawny, thickly clothed with black hairs and bristles; claws black: wings pale brown; wing-ribs and veins pitchy. Length of the body 2 lines [4.2 mm.]; of the wings 6 lines [span of wings, 12.6 mm.]." Austen at first (1903) synonymized the type of *remota* with *O. avicularia*; but in his personal reprint (now at British Mus.) a manuscript note, dated January 17, 1923, and quoted by Crichton (1951), reads as follows: "I now consider *O. remota* Walk., owing to the greater width of its frontal margins posteriorly, to be specifically distinct from *O. avicularia* L." I reached the same conclusion after studying the female type at the Brit. Mus. in 1951; but it was found eventually that *remota* is not separable from the earlier *O. parva* Macquart. The wing of Walker's type, measured by Dr. G. B. Fairchild, is 5.8 mm. long.

Original description of *O. synallaxidis* (Spanish text translated): "Picea, nitida; capite supra rubro-testaceo, utrimque carina depressa, nigro-setosa, posticeque spatio ocellari piceis; mesonoto lineola longitudinali flava; alis modice et uniformiter infumatis; femoribus infra sternoque virescentibus. Long. 4.5 mm. Caput supra rubro-testaceum, utrimque carina depressa, nigro-setosa, posticeque spatio ocelligero piceis, nitidis, infra sordide virescenti-testaceum; os nigro-setosum, labro, bulbo rostrifero lobisque lateralibus albidis, his basi margineque externo palpisque piceis, nitidis, rostro flavescenti. Mesonotum angulis anticis productis, sulculo medio instructum sutura satis profunda, medio interrupta, utrimque et postice nigro-setosum, piceum, nitidum, humeris lateribusque sordide virescenti-testaceis, lineola media flava, in aversum paululatim ampliata, guttulisque duabus subobsoletis, coloris humerorum, prope marginem anticum sitis, ornatum; scutellum piceum, nitidum, transversim striatum, sulculo medio, postice in depressionem latam dilatato, munitum, margine nigro-setosum; pleurae piceae, nitidae; sternum sordide virescenti-testaceum, nitidum; pedes picei, nigro-setosi, femoribus infra coxisque ut sterno, sed illis virescentioribus tarsis anterioribus quoque parum virescenti-testaceis, unguibus nigro-piceis; alae uniformiter infumatae, sed hyalinae, venis piceis, costali nigro-setulosa, basi virescenti; halteres fusciscentes, clava alba. Abdomen fusco-virescens, nigro-setulosum et setosum. Very similar to *O. erythrocephala* Leach and *O. parva* Macq. I have nevertheless decided to regard it as different, because the descriptions of these species do not mention the very distinct line on the mesonotum. In addition Leach calls the color of the abdomen of the first-mentioned species yellow ('luteum'), and Macquart calls the wings of the second-mentioned species 'somewhat yellowish' without mentioning the smoky color visible in those of our *Ornithomyia*." Attempts to trace the present location of the type have failed and it is most probably lost. Although the description mentions little beyond color characters, of doubtful value in the Hippoboscidae, it agrees best, particularly in size, with *Ornithomyia parva*, the common bird-fly of temperate South America. I list it provisionally as a synonym of this species until flies taken on *Asthenes patagonica* in Argentina will settle the matter.

Original description of *O. chilensis* (translated from the Spanish): "Black above, greenish below. Green prevails in life and black after death, because the green occurs in the soft integument between the coriaceous plates and is more visible before the insect shrivels and dries. Green is more extensive below, as well as on the legs. The extent of this tinge differs greatly among the specimens. The description is made from three specimens dead for a week and dry. Head as wide as anterior margin of thorax, depressed between eyes [inner orbits] and posterior elevation carrying the ocelli [postvertex] black and shiny; median depression [mediovertex] dark fulvous; thorax above, main veins of wings, in

anterior and basal areas, black and shiny; 4th, 5th and 6th longitudinal veins less marked and fuscous beyond cross-veins; membrane of wings little transparent, but not infusate. Thorax with a narrow, longitudinal, fulvous median line. Abdomen blackish above, paler at apex than at base. Legs fuscous above, more or less greenish; green prevailing on under side, very pronounced basally. Clearly close to the European *O. avicularia*; but the great geographical distance separating the two and certain color differences induce me to regard them as distinct. Length 5 to 7 mm." The description mentions no character of specific value in *Ornithomyia*. Fortunately, I saw 2 of the 3 original cotypes (♂ and ♀) in 1953 at the California Academy of Sciences. They are unquestionably the species here called *Ornithomyia parva* (= *O. remota*).

Although Speiser proposed *O. paricella* as a substitute name for Reed's *O. chilensis*, he redescribed the species from several specimens, one being from the type host of *chilensis* and most probably the third of Reed's original cotypes, since it was from the type locality. His description reads (translated from the German): "It is one of the smaller species of the genus and is related to *O. anchineuria* m. (= *pallida* Say) [*O. fringillina* Curtis of Europe and North America], owing to both basal cells being exactly the same length; it differs from that species definitely in being darker. The specimens are 4 to 5 mm. long (Reed gives 5 to 7 mm.); the distance from oral margin to hind margin of scutellum is 2.75 to 3 mm. Head rounded; ocellar triangle [postvertex] and eye margins [inner orbits] blackish-brown; clypeus [frons] leather-brown, with a rounded pit. Antennal appendages yellowish, with a black dot at base, bearing black bristles. Maxillary palpi straight, extending little beyond antennal appendages, blackish-brown. Thorax shiny blackish-brown, with a paler longitudinal suture [median notal suture], yellowish-brown pleura and pale yellowish-brown humeral callosities, which bear a dorsal median blackish-brown dot. Legs pitch-brown, darker above. Wings dusky hazel-brown, transparent. Apical section of costa two-thirds the length of penultimate section; 2nd basal cell the exact length of 1st, the cross-veins being placed above each other; anal cell less than half as long as 2nd cell. Abdomen entirely black, with black setae, also on the 4 tougher chitinous plates." I have not seen Speiser's specimens; but, as one of them was possibly a cotype of Reed's *chilensis*, it seems safe to refer them to *O. parva* Macquart, Speiser's description agreeing with what I here call *parva*.

Subgenus *Pseudornithomyia* Lutz, Neiva and da Costa Lima

Pseudornithomyia Lutz, Neiva and da Costa Lima, 1915, Mem. Inst. Osw. Cruz, 7, pp. 176 and 185 (monotypic for *Pseudornithomyia ambigua* Lutz, Neiva and da Costa Lima, 1915).

Ocelli lacking, their position sometimes indicated by one or more small, superficial pits. Prosternal lobes unusually long and narrow, rather pointed triangular.

The original diagnosis of *Pseudornithomyia* (as a genus) was as follows (translated from the Portuguese): "Clypeus [frons] short, emarginate in the middle, almost covered by the hairy antennal appendages, which are tongue-shaped, close together basally and diverging apically. Frons [interocular face] broad; vertex [postvertex] without ocelli. Humeral callosities very large; scutellum elliptical with three rows of setae or hairs; scutellar [pleurotergal] processes subconical. Wings with the veins as in *Orni-*

thoetona, but with microtrichia, except for the bare basal area." Except for the lack of ocelli, these characters are not diagnostic, being found also in some species of *Ornithomyia* not closely related to *O. ambigua*.

The subgenus is known at present from the New World only and comprises 2 species. They are the most specialized members of the genus.

Ornithomyia (Pseudornithomyia) ambigua (Lutz, Neiva and da Costa Lima)

Figs. 31A-E

Pseudornithomyia ambigua Lutz, Neiva and da Costa Lima, 1915, Mem. Inst. Osw. Cruz, 7, p. 185; Pl. 27, fig. 5; Pl. 28, fig. 7 (no sex. Brazil: Minas Gerais, 2 specimens on *Leptotilla rufaxilla reichenbachii*; Santa Catharina, 2 specimens on swallows; holotype and paratypes probably in Inst. Osw. Cruz, Rio de Janeiro). Falcoz, 1930, Encyclop. Entom., Sér. B, Diptera, 5, (for 1929), p. 27 (Brazil). J. Bequaert, 1942, Bol. Entom. Venezolana, 1, No. 4, p. 81; 1943, Jl. of Parasitology, 29, p. 135. Anduze, Pifano and Vogelsang, 1947, Bol. Entom. Venezolana, Num. Extra, p. 6.

Distribution and Specimens Examined. COLOMBIA: Buenos Aires, Depto. Santander Norte, 1♂ on *Notiochelidon c. cyanoleuca* (M.A. Carriker, Jr.); Valdivia, Depto. Antioquia, 1♀ on *Notiochelidon c. cyanoleuca* (M.A. Carriker, Jr.).

VENEZUELA (recorded by Anduze, Pifano and Vogelsang, 1947): Macuto, Caracas, on *Notiochelidon c. cyanoleuca* (N. Dearborn); El Valle, Distrito Federal, near Caracas, on *Iridoprocne albiventer* (C.H. Ballou); La Florida, Distrito Federal, on *Iridoprocne albiventer* (C.H. Ballou); Rancho Grande, between Maracay and Ocu-mare-de-la-Costa, 3500 ft., State of Aragua, 1♀, 1♂ on *Notiochelidon c. cyanoleuca* (W. Beebe).

BRAZIL (recorded by Lutz, Neiva and da Costa Lima, 1915; Falcoz, 1930): São Paulo, on a swallow (J. Lane); Botucatu, State of São Paulo, on *Progne chalybea domestica*; Boraceia, State of São Paulo, on *Xenops r. rutilans*; Repressa, State of São Paulo, on *Stelgidopteryx r. ruficollis*; Sta Tereza, State of Espirito Santo, on *Notiochelidon c. cyanoleuca*.

PERU: Pan de Azucar, Río Tarma, on *Notiochelidon c. cyanoleuca* (W. Weyrauch).

As *O. ambigua* has been taken in several widely separated localities, it probably occurs in all tropical parts of South America, but apparently not north or west of the Isthmus of Panama.

Known Hosts of *O. ambigua* (verified individual records in

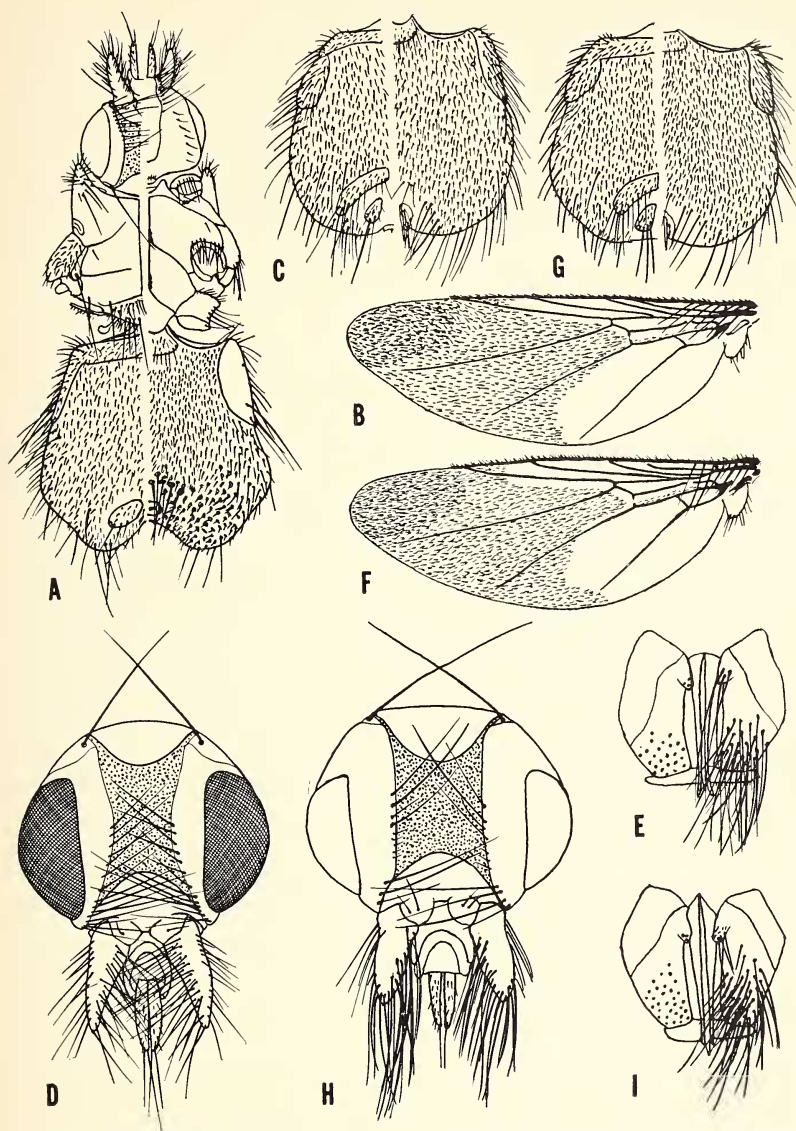


Fig. 31. **A-E**, *Ornithomyia* (*Pseudornithomyia*) *ambigua* (Lutz, Neiva and da Costa Lima), Rancho Grande, on *Notiochelidon c. cyanoleuca*: **A**, body in dorsal and ventral view, ♀; **B**, wing, ♀; **C**, abdomen in dorsal and ventral view, ♂; **D**, head, ♂; **E**, ♂ terminalia. **F-I**, *Ornithomyia* (*Pseudornithomyia*) *hoffmannae* J. Bequaert, Cacahoatán, on *Buteo nitidus plagiatius*: **F**, wing, ♀ holotype; **G**, dorsal and ventral view of abdomen, ♂ allotype; **H**, head, ♂ allotype; **I**, terminalia, ♂ allotype.

parentheses). Columbiformes: *Leptotilla rufaxilla reichenbachii*. Passeriformes (11): *Iridoprocne albiventer* (2); *Notiochelidon c. cyanoleuca* (6); *Progne chalybea domestica* (1); *Stelgidopteryx r. ruficollis* (1); *Xenops r. rutilans* (1).

Ten of the 11 verified records being from swallows (Hirundinidae), the fly is evidently a strict specific parasite of such birds. The records from a pigeon (*Leptotilla*) and an oven-bird (*Xenops*) are either accidental or more probably due to fortuitous contaminations.

Affinities. These are discussed under *O. hoffmannae*. The truly distinctive characters are given in the key. The male terminalia (Fig. 31E) are similar to those of *O. hoffmannae*.

Original description of *P. ambigua* (translated from the Portuguese): "Length of body 5 mm., of head and thorax combined 2.5 mm., of wing 5 mm. General color chocolate, a little reddish over hind part of head and ochraceous over humeral callosities. Head generally ochraceous, mostly infuscated or blackish. Antennal processes rather long, with even longer bristles, entirely chocolate, as are also the palpi. Clypeus short, deeply emarginate medially, with whitish pruinosity and ciliae; frontal triangle medially with a small pit connected with the hind margin by a furrow (these depressions seem to vary somewhat); vertex without ocelli, but with a small pit near middle of side margins. Both triangles [of face] somewhat rounded, shiny, like the ocular margins [inner orbits] which are broad and bear a row of ciliae over anterior half. Frons broad, dull portion [mediovertex] somewhat longer than wide, the four sides rather concave. Occiput oblique, covering anterior part of thorax. Thorax with conical humeral callosities, ochraceous at tip, very long, their base resting in a deep emargination of mesonotum; spiracle distinct as a white, pruinose spot. Median notal suture deep, with reddish margins; transverse mesonotal suture effaced medially; the margins of mesonotum form callosities. Scutellum transversely elliptical, on each side with 4 long bristles between anterior and posterior margins, which bear long hairs. Squamular process dark, subconical. Abdomen chocolate color, with many concolorous hairs. Legs chocolate color or ochraceous-gray, with many scattered hairs; anterior femur very thick. Wings bare from base to tip of costa and to cross-veins, also over axillary cell and most of cell located between anal cross-vein, 4th and 5th veins [error for 5th and 6th, as shown by the figure] and hind margin [the figure shows most of 3rd posterior cell bare]. Veins chestnut or blackish, second cross-vein white over most and third over little of its length." The original figures show the scutellum (Pl. 27, fig. 5) and the wing (Pl. 28, fig. 7). I have not seen any of the types of this species, which is easily recognized from the foregoing description. None of the several specimens I saw had as many and as long weak setae near the anterior margin of the scutellum as shown in the original fig. 5, where the artist, it seems, exaggerated their length and number.

Ornithomyia (Pseudornithomyia) hoffmannae, new species

Figs. 31F-I and 32

Female. Head seen in front as wide as high, subcircular; interocular face at its narrowest nearly 4 times as wide as an eye, almost twice as wide as length of eye; inner margins of eyes very

slightly converging below; inner orbit about half as wide at mid-length as mediovertex, only slightly narrower at ptilinal suture, mostly smooth and bare, with a single inner row of 2 long and 3 shorter bristles on middle third and a few minute setae on lower third; gena about half as wide as inner orbit, with 4 unequal setae, 1 or 2 very long near the frontal suture; 1 long vertical bristle; postvertex long, semi-elliptical, about $\frac{2}{3}$ the length of mediovertex, the anterior margin and sides forming one even curve; occipital margin nearly straight; surface of postvertex smooth, without traces of ocelli and without pit. Eyes relatively short and narrow, about $2\frac{1}{2}$ times as long as greatest width, occupying only the lower $\frac{1}{3}$ of sides of face. Interantennal area of frons very narrow basally, separated from the lunula by a suture, broadly but deeply emarginate anteriorly, the apical arms forming bluntly pointed, finger-shaped lobes. Palpi short, slender, only about $\frac{1}{5}$ of height of head. Antennae: 1st segment partially divided from the lunula by a suture on the outer side only, bearing 2 short setae; appendage of 2nd segment moderately long and narrow, bluntly pointed, 3 times as long as wide, about as long as frons; inner half and apex with many long bristles. Thorax relatively wide and short; mesonotum about twice as wide as long in the middle; anterior margin deeply concave, enclosing posterior $\frac{1}{3}$ of head; antero-lateral areas forming broad humeral callosities, almost completely divided by a suture from precutum, produced anteriorly into bluntly pointed lobes bearing many long and short setae, their surface elsewhere with a few long and short setae anteriorly and one long bristle near outer hind margin (2 or 3 bristles in this position in male allotype); mesothoracic spiracle small, placed dorso-laterally in outer hind corner of humeral callosity; mesonotum with a deep median notal suture from anterior margin to scutellum; transverse mesonotal suture deep, fairly broadly interrupted medially; mesonotum mostly bare, except for one long notopleural bristle, 3 very small presuturals, 3 short postalars and 2 moderately long precutellars on each side; notopleuron with many, mostly long setae over hind third, the outer hind angle short, broadly rounded; integument of dorsum shiny, with a few very fine, superficial wrinkles. Scutellum short and broad, very shallowly, convexly curved behind, with a slight transverse preapical depression bearing a row of 12 long bristles, in 6 pairs; a few small setae basally on the disk and a dense apical fringe. Sternum as usual in *Ornithomyia*; median lobes of prosternum long, narrowly triangular, with blunt apex. Legs without distinctive features; femora moderately setose, more hairy

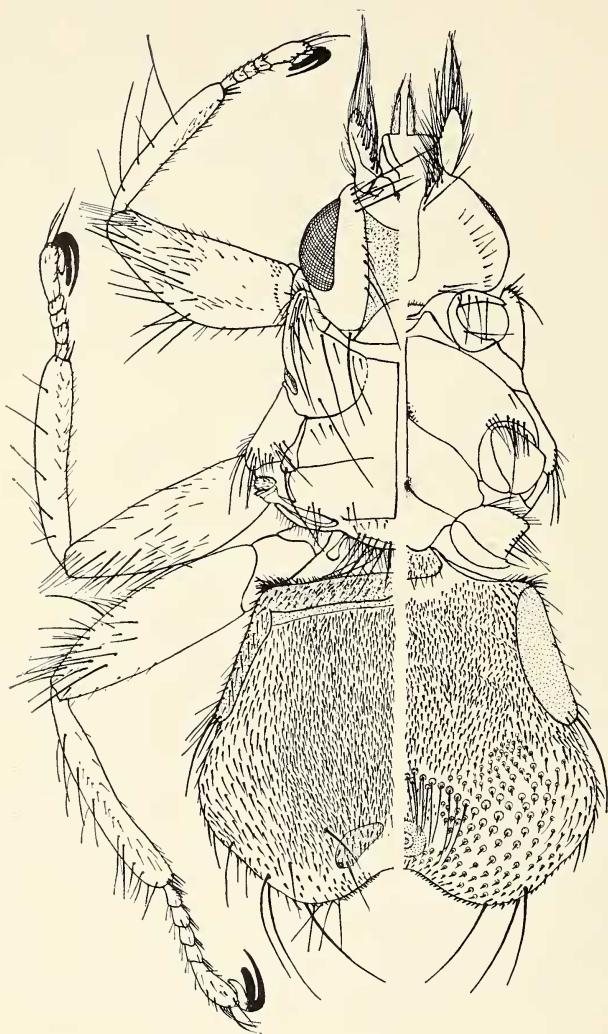


Fig. 32. *Ornithomyia* (*Pseudornithomyia*) *hoffmannae* J. Bequaert, body in dorsal and ventral view, ♀ holotype, Cacahoatán, on *Buteo nitidus plagiatus*. × about 17.

over apical half; tibiae with few long setae spaced in a longitudinal row; mid tibia with 1 and fore tibia with 2 apical spurs; hind tibia with a group of 4 spines at apex. Wing (Fig. 31F) short, more narrowed apically than usual, nearly 3 times as long as greatest width, extensively covered with microtrichia over nearly entire 1st and 2nd posterior, and apical third of 3rd posterior cells, as well as narrow tip of axillary cell; veins crowded in antero-basal part of wing; cells narrower and relatively shorter than usual, particularly the 1st and 2nd basal cells; posterior cross-vein basad of anterior cross-vein; anal cross-vein at about mid-length of 2nd basal cell; costa extending a short distance beyond tip of 3rd longitudinal (more than usual in *Ornithomyia*); tip of subcosta not connected with costa (probably abnormal); basal portions of 4th, 5th and 6th longitudinal veins forming thick, short stumps beyond which the veins are very weak and hyaline; costa with many very short setae and, over basal $\frac{1}{4}$, with some very long bristles; other veins bare. Abdomen with a short sclerotized basal tergite continued on each side as a narrow plate, the tergite bearing a few minute hairs and some stronger setae along anterior margin; apices of lateral extensions with one very long, stiff bristle and a few shorter setae; a median pair of small, irregularly oval sclerites near apex, each bearing a few short setae and one long bristle, as well as a spiracle; remainder of dorsum soft, membranous, without sclerites, fairly uniformly covered with minute setae, a few of them longer at sides, and with a few very long, stiff preapical bristles; no ventral sclerotized areas, except for the lateral extensions of the basal dorsal sclerite; basal half of venter covered fairly uniformly with minute setae; setae of apical half much thicker, each on a raised papilla; the papillae large, knob-like and with long, stiff bristles over the median area some distance basad of anal and genital openings.

Length of head and thorax (from notch of frons to hind margin of scutellum), 2.8 mm.; of wing, 4.5 mm.; width of wing, 1.6 mm. (total length of specimen in alcohol, 4.8 mm.).

Male. Similar to the female, except as follows. Subcosta ending in costa. Abdomen (Fig. 31G): a pair of short and broad (transverse), postero-median dorsal sclerites, in close contact medially (homologous with the 3rd median sclerite of *O. fringillina*), each bearing 8 or 9 long bristles at side near hind margin, as well as some small setae; apicad of these, a median pair of smaller, oblique sclerites, each with a spiracle, 3 long bristles and some short setae (homologous with apical pair of female); ventrally without

setigerous knobs, but covered fairly uniformly with short setae, and a few long bristles at apex and sides. Male terminalia (Fig. 31I) similar to those of other species of *Ornithomyia*, but the gonocoxites rather broad and short, bearing 3 short bristles and a few minute setae; the lateral plates more sclerotized than usual and with many long bristles. Measurements as in female.

MEXICO: Cacahoatán, State of Chiapas, 600 m., 1 female holotype and 1 male allotype, on *Buteo* (*Asturina*) *nitidus plagiatus* (Collector unknown.—Received from Dr. Anita Hoffmann Sandoval). Holotype at Escuela Nacional de Ciencias Biológicas, México, D.F.; allotype at Mus.Comp.Zool., Cambridge, Mass.

Affinities. Although closely related to *O. ambigua* and belonging in the same subgenus, *O. hoffmannae* is easily distinguished by the characters given in the key. The wider face and relatively smaller eyes are particularly striking. The differences in the bristles and setae on the inner orbits, scutellum and abdomen are possibly not fully reliable, as only one pair of the new species is available.

Crataerina v. Olfers, 1816

- Crataerina* v. Olfers, 1816, De Vegetativis et Animatis Corporibus in Corporibus Animatis Reperiundis Commentarius, 1, p. 101 (monotypic for *Crataerina lonchoptera* v. Olfers, 1816 = *Ornithomyia pallida* Latreille, 1812).
- Crataerhina* Speiser, 1900, Ann. Mus. Civ. Stor. Nat. Genova, 40, p. 555 (emendation of *Crataerina* v. Olfers; same type).
- Crataerrhina* Bezzi, 1904, Kat. Paläarkt. Dipt. 4, p. 280 (emendation of *Crataerina* v. Olfers; same type).
- Crathaerina* Hesse, 1919, JI. f. Ornithologie, 67, p. 408 (error for *Crataerina* v. Olfers; in the combination *Crathaerina pallida* "Olivier").
- Cratarrhina* Jobling, 1926, Parasitology, 18, No. 3, p. 341 (error for *Crataerina* v. Olfers, with *Oxypterum* Leach as synonym).
- Crathaerrhina* Hardenberg, 1927, Bijdrage tot de Kennis der Pupipara, p. 35 (error for *Crataerina* v. Olfers).
- Crahterina* Huzimatu, 1938, Science Repts. Tohoku Imperial Univ., Sendai, (4), Biol., 13, pt. 1, p. 59 (error for *Crataerina* v. Olfers).
- Crathaerhina* Eichler, 1939, Zeitschr. Hyg. Zool., 31, p. 215 (cited as a misspelling of *Crataerina* v. Olfers).
- Craterrhina* and *Craterhina* Brauns, 1939, Zool. Jahrb., Abt. Physiol., 59, p. 334, footnote (cited as misspellings of *Crataerina* v. Olfers, according to Eichler, in litt.).
- Cratoerina* [Anonymous], 1951, Nature, London, 167, p. 937 (in the combination *Cratoerina pallida*; error for *Crataerina*).
- Oxypterum* "Kirby, MS" Leach, 1817 (September), Gen. Spec. Eproboscideous Ins., pp. 3, 5, 7 and 17 [1818, Mem. Werner. Soc. Edinburgh, 2, pt. 2, pp. 549, 551, 553 and 563] (for *Ornithomyia pallida* "Olivier" [really of Latreille, 1812] and *Oxypterum kirbyanum* Leach, 1817, both one species); 1817 (November), in Brewster's Edinburgh Encyclopaedia, 12, pt. 1, p. 162 (with brief diagnosis: "ocelli none." Monotypic for *Oxypterum kirbyanum* Leach). Type by designation of Westwood, 1840,

- Introd. Modern Class. Ins., 2, Generic Synopsis, p. 154: *Oxypterum kirbyanum* Leach, 1817 = *Ornithomyia pallida* Latreille, 1812.³⁴
- Ocypterum* Bigot, 1885, Ann. Soc. Ent. France, (6), 5, p. 234 (either emendation or misspelling of *Oxypterum* Leach, 1817, which spelling is used on p. 229).
- Oxypterum* Charbonnier, 1920, Proc. Somersetshire Archaeol. Nat. Hist. Soc., 65, p. 96 (error for *Oxypterum*).
- Anapera* Meigen, 1830, Syst. Beschreib. Europ. Zweifl. Ins., 6, p. 234 (substitute name for *Oxypterum* Leach, 1817, including the same two species; type by present designation: *Ornithomyia pallida* Latreille, 1812).
- Chelidomyia* Rondani, 1879, Bull. Soc. Ent. Italiana, 11, p. 15 (for 4 species: *C. pallida* Leach, 1817; *C. melbae* Rondani, 1879; *C. hirundinis* Linnaeus, 1758; and *C. cypseli* Rondani, 1879; with *Stenopteryx* Leach, *Oxypterum* Leach, *Crataerina* v. Olfers, and *Anapera* Meigen as synonyms; type by present designation: *Ornithomyia pallida* Latreille, 1812).
- Chelyidomyia* Bezzi, 1891, Bull. Soc. Ent. Italiana, 23, p. 90 (in the combination *Chelyidomyia pallida*; error for *Chelidomyia* Rondani).
- Although obviously a variant of *Crataerina*, *Craterina* Samouelle, 1819 (The Entomologist's Useful Compendium, p. 303), is not included in the foregoing synonymy, because it was used only in the combination *Craterina hirundinis* L., a species of *Stenopteryx*. Later English authors (Curtis, 1826, 1829; Kirby and Spence, 1828; Stephens, 1829; Westwood, 1840; Walker, 1849) all seem to have used *Craterina* in the same sense, for *Stenopteryx hirundinis*; although some of them may have confused *S. hirundinis* and *Crataerina pallida*.

Generic Characters. Parasites of birds, with reduced, non-functional wings, not metallic-greenish; but a dull-green pigment in the haemolymph may show through the integument in life. Head as high as wide or higher, deeply inserted between the prominent humeral callosities. Ocelli absent. Eyes small, occupying dorso-laterally $\frac{1}{2}$ of the height of the head or less, each less than $\frac{1}{2}$ the width of the interocular face, with many minute but distinct ommatidia. Postvertex and frons far apart. Upper part of postvertex a thin, translucent plate along the strongly arched occipital margin, which covers anterior margin of prescutum. Suture between lunula and interantennal area of frons usually lacking or incomplete, rarely complete; lunula without median pit or depression, longer than interantennal area; apical arms of frons rather short, slightly diverging; when the proboscis is fully extended, the sclerotized clypeus, bearing a few setae, is visible in certain species (Figs. 34J; *C. pallida*), but not in others. Antennae medium-sized, about as in *Ornithomyia*: 1st segment with 2 or more setae, separated by a complete or incomplete suture from lunula; 2nd

³⁴ The binomial *Oxypterum kirbyanum* was also published by Kirby and Spence, 1817 (month ?), Introduction to Entomology, 2, [p. 350] in the explanation of Pl. 5, fig. 1. The plate itself is dated January 1, 1817, but bears no name and probably appeared much before the Explanation.

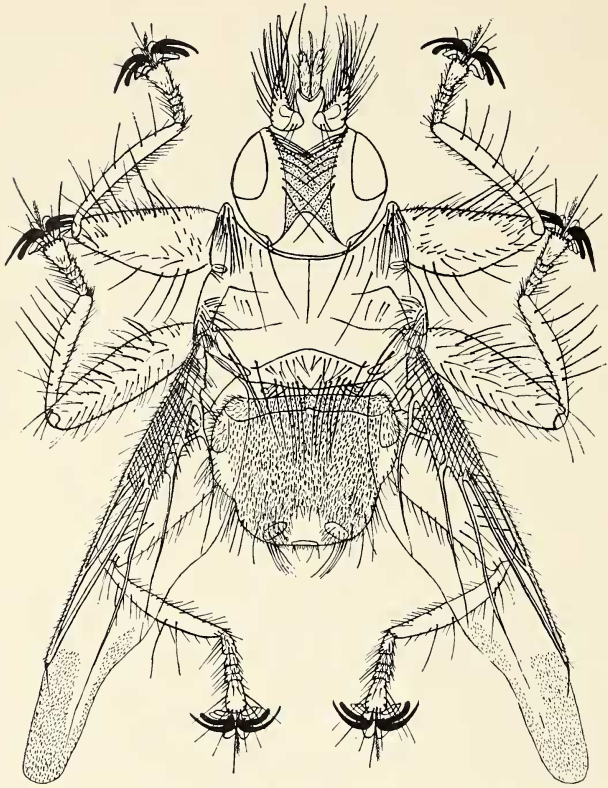


Fig. 33. *Crataerina seguyi* Falcoz, ♀, Tofo, on *Notiochelidon cyanoleuca patagonica*. $\times$ about 17.

segment with a moderately long and narrow appendage, gradually narrowed from the base to the blunt point, which does not reach tips of palpi; both appendages diverging, leaving apical arms of frons and palpi fully exposed; arista flattened, gradually widened and slightly spatulate, the surface with very fine ridges spreading fan-like from the base. Palpi well-developed. Thorax short and broad, sometimes twice as wide as long in the middle, very flat, depressed or even slightly concave in the center. Pronotum very short, not visible from above. Humeral callosities large, strongly produced forward as blunt, triangular lobes, extending along upper $\frac{1}{3}$ of head to near upper eye margins; posthumeral suture either lacking or short and restricted to side; prothoracic spiracle medium-sized, entirely dorsal, close to outer hind margin of callosity. An-

terior margin of prescutum deeply and evenly curved inward, semi-elliptical; transverse mesonotal suture curved forward medially where it is very briefly interrupted, placed at hind third of mesonotum; anterior ridge of parascutellum fused with mesoscutum; median notal suture distinct anteriorly, not reaching scutellum; notopleuron either completely fused with prescutum or set off posteriorly only by a slight depression; dorsal portion of anepisternum broadly lathe-shaped, with blunt outer hind edge, divided on outer side only by a crested suture from humeral callosity, either fused with mesonotum or separated from it by a weak suture. Scutellum short, but broad; scuto-scutellar suture convexly curved forward medially; hind margin very slightly convex or nearly straight, somewhat raised and set off by a narrow, transverse, pre-apical groove. Metathoracic pleurotergite moderately and uniformly convex, not visible from above. Halteres present, well developed. Sternum (Fig. 34A): basisternum of prothorax separated from mesosternum by a complete suture, divided into 2 short, broadly triangular, bluntly conical intercoxal lobes; mesosternum, metasternum and longitudinal sternal suture as in *Ornithomyia*; no metasternal spur near hind coxa. Metathoracic spiracle placed as in *Ornithomyia* and *Ornithoctona*. Legs long, very robust; femora much swollen; tibiae flattened, relatively narrow; tarsal segments 1 to 4 broad, short; hind basitarsus shorter than in *Ornithomyia*, at most twice the length of 2nd segment, beneath with many spine-like bristles partly in a basal transverse row; tips of all tibiae normal; tibial spurs replaced by an apical row of 2 to 5 short, stiff bristles. Claws (Fig. 34F) symmetrical in each pair, deeply split (seemingly tridentate): terminal (outer) tooth long, very slender, sharp; inner tooth shorter, flattened, blade-like, with pointed or rounded tip; in addition a slender, tooth-like basal "heel," slightly shorter than inner tooth; 2 pad-like pulvilli and a long, feathered empodium. Wing (Figs. 34B-C) either of about normal length or somewhat shortened, always partly narrowed; basal $\frac{1}{2}$ to $\frac{2}{3}$ much wider than the abruptly narrowed apical portion, which varies in length even in the same species. Venation variable, even intraspecifically, hence not reliable for specific diagnosis; when most normal, nearly as complete as in *Ornithomyia*; subcosta thin, complete; longitudinal veins crowded in anterior half and cross-veins moved to basal third of wing, more so in certain species; some veins thickened or coalescent, partly obliterating certain cells, or supernumerary veins appear; costa covered with fine, short setae and a dense row of many long bristles reclining over the wing;

one stiff, long bristle at tip of costa (often broken off); other veins bare; membrane mostly bare, in some species the narrowed tip with very small microtrichia; 1st basal cell (when normal) longer than 2nd; anal cell about half the length of 2nd basal, with acute upper apical angle; posterior basal cross-vein sometimes partly aborted; alula completely fused in most cases with membrane proper, the hind base of wing unusually wide basad of anal cell (occasionally a short notch marks the limit of the alula); calypteres rudimentary; halteres present, small. Abdomen: dorsum in some species with, in others without unpaired, small, median sclerites behind the fused basal pleurotergites; in all species posteriorly with preapical tergites, one pair in female, two pairs in male (sometimes fused in a pair); ventrally with only a short, semi-elliptical basal sternite; no striated median, dorsal area. Body very setulose or bristly, particularly on 2nd antennal segment, humeral callosities, anepisternum, scutellum, legs and abdomen; mesonotum and sternum with few setae; 9 or 10 orbital bristles in one regular, continuous row from edge of frontal suture to about mid-height of face; 1 vertical bristle (exceptionally 2); 1 notopleural bristle on a well-defined lobe; 5 or 6 pairs of long bristles on scutellum in 1 or 2 irregular preapical rows, in addition to scattered setae on the disk. Male terminalia as in *Ornithomyia* and *Ornithoetona*; gonocoxites reduced to a pair of rudimentary lobes each bearing 2 bristles.

The puparium of *C. pallida* (Figs. 34G-I) was described by Johnsen (1948, p. 285, fig. 9). According to specimens from swifts' nests in London, sent by Mr. G.E. Woodroffe, it is very broadly oval or nearly elliptical in outline, slightly depressed and equally convex dorsally and ventrally, with the side edges very broadly rounded, about 3.8 mm. long, 3.4 mm. in greatest width and 2.8 mm. thick. The posterior cap bearing the peripneustic lobes is scarcely raised, not notched medially, about as high as wide, hexagonal with broadly rounded angles. The relatively few spiracular pores are arranged in a curve like an irregular question-mark on each of the six radiating areas of the cap, which are not set off by depressions. The integument is bare, smooth, with a microscopic maze of very fine engraved lines. At the anterior end, the semi-circular seam is fairly well marked, but the circular seam is distinct only at the sides where it meets the semi-circular seam. A few puparia I have seen of *C. seguyi* scarcely differ from those of *C. pallida*, except in size.

Crataerina occurs in both the Old and New World. It is most

widely distributed in the Old World, where some 8 species have been described; but how many of these will eventually be retained as valid is uncertain. The only species known from America is strictly tropical.

Crataerina and *Stenepteryx* Leach (1817) are very closely related and there is a question whether they should be kept as distinct genera. If they were combined, *Stenepteryx* could be treated as a subgenus of *Crataerina*. The single known *Stenepteryx*, *S. hirundinis* (Linnaeus), is a strictly Palearctic parasite of Hirundinidae (Part I, p. 316). It appears to be somewhat less specialized than the species of *Crataerina*, from all of which it differs in the relatively broader and shorter head (Fig. 4D), the proportionately larger eyes, the smaller postvertex, the slightly less aberrant venation, as well as in the characters of wings and ocelli mentioned in the key to the genera. These peculiarities are of minor importance and, among the Hippoboscidae in general, of specific rather than generic value.

Crataerina seguyi Falcoz

Figs 33 and 34A-F

Crataerina seguyi Falcoz 1930, Encyclop. Entom., Sér. B, Diptera, 5, (for 1929), p. 53, fig. 8 (♂; no host. Peru: Arequipa. Type at Paris Mus.). J. Bequaert, Rev. Acad. Colombiana Cienc. Ex. Fis. Nat., 3, No. 12, p. 416. Anduze, Pifano and Vogelsang, 1947, Bol. Entom. Venezolana, Num. Extra, p. 6 (Venezuela). Schuurmans Stekhoven, 1952, Beiträge zur Fauna Perus, 3, Wissensch. Bearbeit., pp. 95 and 101.

Crataerina seguyi J. Bequaert, 1951, Agricultura Técnica, Santiago de Chile, 10, (for 1950), p. 9 (error for *C. seguyi*).

Distribution and Specimens Examined. COLOMBIA: Bogotá, ♀ on *Notiochelidon murina* (Hno. Apolinar-María); La Picota near Bogotá, ♀ and ♂ from the eaves of a house (Hernando and Ernesto Osorno M.); Piedecuesta, Depto. Santander Sur, on *Notiochelidon murina* (M.A. Carriker, Jr.).

VENEZUELA (recorded by Anduze, Pifano and Vogelsang, 1947, after my determination): Apartaderos, State of Mérida, 3320 m., ♂ bred from puparium found in a swallow's nest (P. Anduze).

PERU (recorded by Falcoz, 1930): Tarma, Depto. Junín, 3000 m., Jan. 10, ♂ on *Notiochelidon murina* (W. Weyrauch); Arequipa (type ♂ at Paris Mus.); Culluhay, Valle Chanchamayo, 3500 m. (J. Ortiz de la Puente).

ARGENTINA: Tunuyan, Mendoza, ♀ and ♂ on *Notiochelidon cyanoleuca patagonica*, March 24, and ♀ on *Alopochelidon fuscata*, March 29 (A. Wetmore); Los Médanos, Hualfín, Catamarca, ♀, ♂

and 2 puparia, on *Notiochelidon cyanoleuca patagonica*, Oct. 4, and ♀ on *Alopochelidon fuscata*, Oct. 4 (S. Pierotti).

CHILE: El Recreo, ♀, Jan. 29 (A. Faz); Putre, Arica, 3550 m., on *Notiochelidon cyanoleuca patagonica* (D. Barros); Tofo, ♀ and ♂ on *Notiochelidon cyanoleuca patagonica* (T. Hallinan).

C. seguyi will probably be recognized as a common South American fly when the ectoparasites of swallows are more carefully studied. Presumably it does not extend north or west of the Isthmus of Panama.

Known Hosts of *O. seguyi* (verified individual records in parentheses). Passeriformes (9 and 1 unidentified swallow): *Alopochelidon fuscata* (2); *Notiochelidon cyanoleuca patagonica* (4); *N. murina* (3).

Bionomics. All known records being from swallows (Hirundinidae), there can be no doubt that these birds are the normal breeding hosts of the American *C. seguyi*. This is most remarkable, as in the Old World the genus *Crataerina* is specific of swifts (Apodidae in the order Apodiformes; see Part I, pp. 267-268 and 316). The few trustworthy European records of *C. pallida* from swallows or other birds are certainly due to accidental straying. It is difficult to account for the different choice of hosts in the two Hemispheres, particularly as numerous presumably suitable swifts are available in the New World also. The Recent species of *Crataerina* may be survivors of two ancestral groups which evolved independently in the two Hemispheres from *Ornithomyia*-like parasites of Hirundinidae, similar to the *Ornithomyia biloba* group of the Old World and the subgenus *Pseudornithomyia* of the New. The New World species kept to the ancestral swallow hosts, while in the Old World they shifted to swifts, becoming somewhat more specialized as a result. The New and Old World species are now obviously congeneric, so that this may be a case of parallel or convergent evolution. However, an alternative explanation is perhaps more probable. The American *C. seguyi*, seemingly less evolved than its Recent congeners, may be the sole survivor of a more primitive and world-wide parasite of swallows, which in the New World was more conservative and remained faithful to the original type of hosts. In the Old World, a more prolific evolution produced species better adapted to the speedier and more aerial swifts, the shift from swallows to swifts possibly induced by a relative abundance of swifts at the time evolution of the flies was most active.

Two apparently normal, black puparia, found with adults associated with *Notiochelidon c. patagonica*, at Los Médanos, scarcely

differ from those of *C. pallida*, as described above, except in size. The larger one is 2.8 mm. long, 1.9 mm. wide, and 1.7 mm. thick.

Affinities. The following notes supplement the original description, which was admittedly incomplete.

Female. Head relatively shorter than in *C. pallida*, about as high as wide and nearly circular. Eyes somewhat larger than in *C. pallida*. Interantennal area of frons much narrower than in *C. pallida*, superficially divided from lunula by a slight depression (deeper at sides), without suture. No trace of clypeus in the membranous area connecting the apical notch of frons with base of palpi. Antennae: 1st segment completely divided by a weak suture from lunula, with 2 short setae; 2nd segment narrower and more pointed than in *C. pallida*, though blunt at tip, with fewer and shorter bristles. Humeral callosities shorter and broader than in *C. pallida*, with a short posthumeral suture; notopleuron fused with mesoscutum; dorsal portion of anepisternum completely divided from mesoscutum, its outer hind edge not projecting (markedly produced in *C. pallida*). Scutellum longer than in *C. pallida*; scuto-scutellar suture more arched. Sternum (Fig. 34A) with the suture between basisternum of prothorax and mesosternum very fine. The narrowed part of the wing (beyond tip of costa) varies from $\frac{1}{6}$ to $\frac{1}{4}$ of the total length; it was shorter than average in Falcoz' type; the transition between the narrow tip and the broader section is more gradual than in most other species of the genus. Some variations in venation are shown in Figs. 33 and 34B-C, but there are many others; subcosta (not shown by Falcoz) present, but very thin. Microtrichia present in the narrow apical area, extending only a short distance basad of tip of costa. Abdomen dorsally without median sclerites between the broad basal sclerotized area and the pair of small preapical sclerites. Length of wing 3.2 to 3.6 mm.; from tip of apical arms of frons to hind margin of scutellum, 1.8 to 2.2 mm. The smallest known species of the genus.

Male. Agreeing with female except as follows: Abdomen (Fig. 34D) dorsally with a short, broad, transverse, slightly curved, median sclerite, bearing several long bristles in an irregular row; apicad of this with the usual pair of small, oblique sclerites, each bearing a long bristle and a spiracle near the outer margin. Male terminalia without peculiarities. Size as in female.

The wings of the ♀ from Tofo, shown in Fig. 33, have the normal venation. In Falcoz' type the 2nd basal cell was abnormally short. In Fig. 34B the 2nd basal cell is obliterated over the apical half

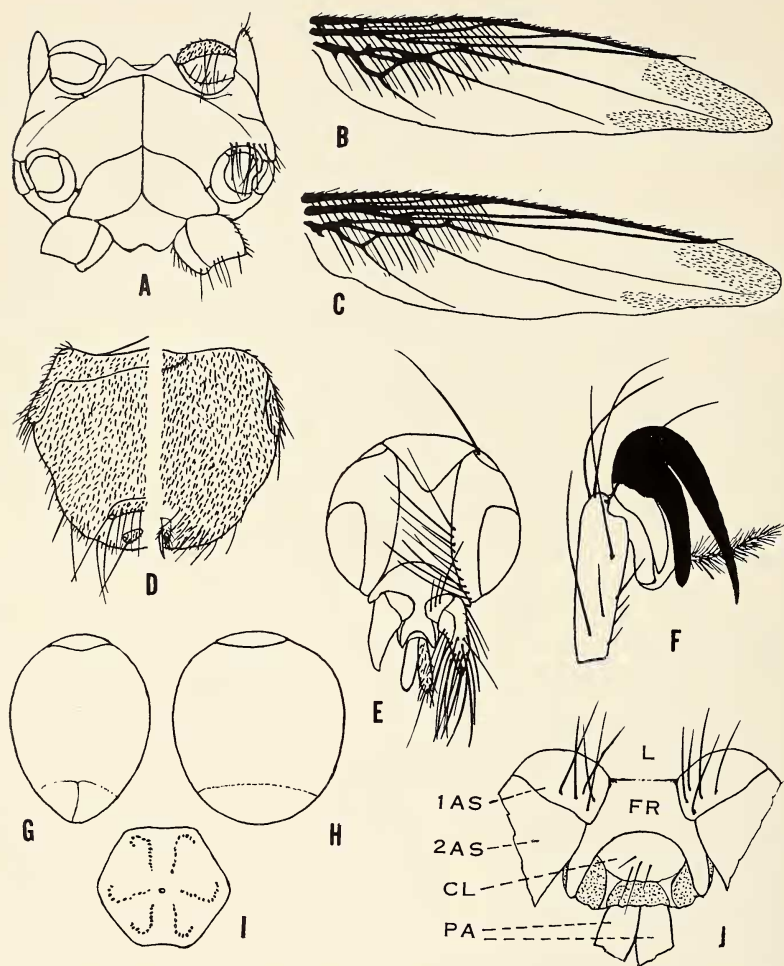


Fig. 34. **A-F**, *Crataerina seguyi* Falcoz; **A**, **D**, **E** and **F** from Tarma, on *Notiochelidon murina*; **B**, from Tunuyan, on *Notiochelidon cyanoleuca patagonica*; **C**, from Putre, on *N. c. patagonica*: **A**, sternum, ♂; **B**, wing, ♂; **C**, wing ♀; **D**, abdomen dorsally and ventrally, ♂; **E**, head, ♂; **F**, distitarsus and claw of hind leg, ♂. **G-J**, *Crataerina pallida* (Latreille): **G-I**, puparium, London, in side view (**G**), from above (**H**), and respiratory lobes (**I**); **J**, lower frontal area and clypeus, ♀, Waldheim, Germany: **1AS** and **2AS**, 1st and 2nd antennal segments; **CL**, clypeus; **FR**, frons; **L**, lunula; **PA**, palpi.

and narrowed over the remainder by thickening and fusion of the 4th and 5th longitudinals; this occurred in both wings of the specimen; but a ♀ taken with it on the same host had a normal venation in both wings. In Fig. 34C the 1st basal cell is divided by a broad fusion of the 3rd and 4th longitudinals; again this was present in both wings. This ♀ from Putre also has some traces of green pigment in the veins.

Original description of *C. seguyi* (translated from the French): *Male*. "Length of body, from base of antennae to tip of abdomen, 4 mm.; of wings 3.3 mm.; width of wings, 1 mm. Color fulvous-olive. Head: parafrontal [orbital] and antennal bristles rather long, black; antennae shaped as in *C. pallida*; frontal vitta [mediovertex] slightly narrowed behind; occipital triangle [postvertex] very distinctly angular in front. Wings: bristles of costa moderately long over basal third, short over remainder of length; distal part of wing narrowed for about one-sixth of total length, apex broadly rounded; tip of 4th longitudinal (M_{1+2}) extending very slightly beyond end of costa; inner margin of wing wavy beyond mid-length; 2nd basal cell narrow, a little longer than anal cell. Owing to the dry condition of the type, it is not possible to see the details of structure of the abdomen. This species is clearly distinct from its congeners in the small size, the shape of the occipital triangle [postvertex], and the shape and peculiar venation of the wings." I have examined the type at the Paris Museum in 1951.

Myiophthiria Rondani

Myiophthiria Rondani, 1875, Ann. Mus. Civ. Stor. Nat. Genova, 7, p. 464 (monotypic for *Myiophthiria reduvioides* Rondani, 1875).

Myiophthiria Rondani, 1878, Ann. Mus. Civ. Stor. Nat. Genova, 12, p. 153 (author's emendation of *Myiophthiria*; same type).

Myiophtheria Galli-Valerio, 1909, Centralbl. Bakt. Parasitenk., Abt. I, Originale, 51, p. 539 (in the combination *Myiophtheria reduvioides* Rondani; error for *Myiophthiria*).

Myiocoryza Rondani, 1878, Ann. Mus. Civ. Stor. Nat. Genova, 12, p. 155 (monotypic for *Myiophthiria lygacoides* Rondani, 1878).

Generic Characters. Parasites of birds, with greatly reduced, non-functional wings, not metallic-greenish, but sometimes with a dull-green pigment in the haemolymph showing through the integument in life. Head (Figs. 35C and 36) deeply inserted between humeral callosities, as high as wide to much higher, subcircular or vertically elliptical. Ocelli absent. Eyes very small, occupying dorsally $\frac{1}{4}$ or less of height of head, each less than $\frac{1}{6}$ of width of interocular face, placed far from frons and much farther from postvertex, with several minute, but distinct ommatidia. Postvertex and frons far apart. Occipital margin moderately to strongly arched, covering anterior margin of prescutum. Frons unusually long, occupying about $\frac{1}{2}$ or more of height of head; interantennal area very broad; apical portion broadly emarginate, with slightly diverging or nearly parallel apical arms; lunula often with a minute pit close to the more or less developed or obsolete suture

separating it from interantennal area. Inner orbits very wide, particularly in upper half of head, where they narrow the mediovertex. Clypeus sometimes present as a minute sclerite in the rostrum membrane between the edge of the frontal notch and the bases of the palpi. Soft mediovertex wrinkled by 8 to 10 parallel, longitudinal, shallow grooves. Antennae medium-sized, not much larger than in *Ornithomyia*: 1st segment partly fused with lunula, bearing several long setae; 2nd segment with a moderately long and wide appendage, bluntly pointed or broadly rounded at apex, not or barely reaching tips of palpi; both appendages scarcely diverging, but leaving apical arms of frons and palpi fully exposed; arista flattened, elongate spatulate. Palpi well developed, but short. Thorax short, broad, nearly twice as wide as long in the middle, very flat, depressed or even somewhat concave medially. Pronotum very short, not visible from above. Humeral callosities large, broad, either bluntly pointed or lobular, extending along upper $\frac{1}{3}$ of head. Posthumeral suture very short, but deep at extreme sides, deflected backward. Prothoracic spiracle large, dorsal, close to outer hind margin of callosity. Anterior margin of prescutum very deeply and evenly curved inward (concave), almost semi-circular; transverse mesonotal suture vestigial at sides only or lacking, when present placed far back at about hind fourth of mesonotum; anterior ridge of parascutellum fused with mesoscutum; median notal suture either lacking or incomplete; notopleuron and dorsal portion of anepisternum fused with prescutum; anepisternum divided by a weak suture from humeral callosity, its outer hind edge prominent, but broadly and evenly rounded. Scutellum very wide and short, transverse; hind margin and deep scuto-scutellar suture either slightly arched or nearly straight, sometimes almost parallel; disk with a superficial, transverse pre-apical groove. Metathoracic pleurotergite a short, conical, blunt protuberance. Halteres present, well developed. Sternum (Fig. 35A): basisternum of prothorax and mesosternum either fused or divided by a very superficial suture; basisternum forming 2 short, broadly triangular, bluntly rounded intercoxal lobes; mesosternum, metasternum and longitudinal sternal suture as in *Ornithomyia*; no metasternal spur near hind coxa. Metathoracic spiracle between pleurotergal protuberance and hind coxa. Legs long, robust, more so in the American than in the Old World species; femora uniformly thick throughout; tarsal segments 1 to 4 broad, short; hind basitarsus as in *Crataerina*; tips of all tibiae normal; tibial spurs replaced by several short, stiff bristles. Claws (Fig. 35F) sym-

metrical in each pair, more deeply divided than in *Crataerina* (seemingly tridentate); inner tooth nearly as slender as and little shorter than outer (terminal) tooth; basal "heel" also slender, tooth-like, almost as long as inner tooth; 2 broad, pad-like, bare pulvilli and a long, feathered empodium. Wing (Figs. 12A, 35B and G) reduced to a short pad, at most twice as long as wide and often only about as wide as long; venation reduced to a few thickened veins crowded in anterior half, owing in part to fusion of some of the original veins, most of which cannot be traced; costa with many long, stiff bristles; other veins usually bare; membrane rather tough, bare; alula fused with base of wing or absent; no calypteres. Abdomen: dorsally with only the basal transverse sclerite in some species; in others in addition with a pair of small preapical sclerites and 1, 2 or 3 mostly small, median sclerites; ventrally with only the small median basal sclerite; no striated median dorsal area. Body unusually bristly, more so than in any other hippoboscid, hence more spider-like; bristles particularly long and numerous on palpi, antennae, inner orbits, sides of thorax dorsally, scutellum and legs; abdomen densely setulose, with many longer bristles along the sides; a group of 3 or more long vertical bristles; 1 notopleural bristle; scutellum with one or more irregular rows of preapical bristles across the width, the disk without short setae. Male terminalia (Fig. 35E) as in *Crataerina*; gonocoxites reduced to very short, bristly lobes; penis valves (claspers) heavy, rod-like as usual in Hippoboscidae. Puparium unknown.

As here understood, *Myiophthiria* comprises all known 4 species of bird-flies with the wings reduced to short pads, all specific parasites of swifts (Apodidae) and swallows (Hirundinidae), and among the most specialized of the Hippoboscidae. They occur in the Oriental Region, the Pacific area, western North America and northern South America, and seem to form 2 natural groups, here given subgeneric rank. *Myiophthiria*, proper, comprising the Old World species, *M. reduvioides* Rondani (1875) (= *capsoides* Rondani, 1878) and *M. lygaeoides* Rondani (1878), is the less specialized type. As compared with the American subgenus *Brachypteromyia*, the dorsal thoracic sutures are more distinct; the scutellum longer and narrower; the legs more slender, with narrow tibiae; the body less hirsute, the primitive muscoid chaetotaxy being easier to trace; the wing pads longer and narrower, with more of the venation retained; and the dorsum of the abdomen with at least a pair of distinct preapical and sometimes also with median sclerites.

Subgenus *Brachypteromyia* Williston, 1896

- Brachypteromyia* Williston, 1896, Ent. News, 7, p. 184 (monotypic for *Brachypteromyia femorata* Williston, 1896 (= *Anapera fimbriata* Waterhouse, 1887).
Brachyptomyia Speiser, 1907, Ent. News, 18, p. 104 (error for *Brachypteromyia*).
Brachypteromia Aldrich, 1907, Jl. New York Ent. Soc., 15, p. 6 (error for *Brachypteromyia*).
Brachypteromyia Anduze, Pifano and Vogelsang, 1947, Bol. Entom. Venezolana, Num. Extra, p. 6 (error for *Brachypteromyia*).

Differs from *Myiophthiria*, proper, in the dorsal sutures of the thorax being either incomplete, vestigial or lacking; the broader and shorter scutellum; the more hirsute body and legs; a further reduction of the abdominal sclerites; the more robust legs, with thicker femora and wider, flatter tibiae; and the shorter and broader wings, with even more reduced venation.

Ferris (1928c) pointed out that *Brachypteromyia* did not differ sufficiently from *Myiophthiria* to be recognized as a distinct genus and he regarded the former as purely a synonym of the latter. It seems useful to retain *Brachypteromyia* with subgeneric rank for the two American species, as they appear to be more evolved than those of the Old World.

Key to American Species of *Myiophthiria*

1. Head $1\frac{1}{2}$ times as long (from apex of frons to occipital margin) as its greatest width. Humeral callosity wide throughout, lobular, broadly rounded at tip. Larger species, 5.5 mm. or more from apex of frons to hind margin of scutellum *M. neotropica*
- Head scarcely longer than its greatest width. Humeral callosity triangular, narrowed anteriorly to a blunt point. Smaller species, at most 3.5 mm. from apex of frons to hind margin of scutellum *M. fimbriata*

Myiophthiria (*Brachypteromyia*) *fimbriata* (Waterhouse)

Figs. 35A-F

- Anapera fimbriata* Waterhouse, 1887, Proc. Zool. Soc. London, p. 164, fig. (on p. 163) (no sex. New Mexico: Fort Wingate, on "*Cypselus melanoleucus* [*Aëronautus s. saxatilis*]. Type in Brit. Mus.). Shufeldt, 1887, The Ibis, London, (5), 5, p. 157, footnote; 1894, The Auk, 11, p. 186. Aldrich, 1923, Insecutor Insectiae Menstruus, 11, p. 78.
Brachypteromyia fimbriata Speiser, 1899, Wien. Entom. Zeitg., 18, p. 202, footnote; 1900, Ann. Mus. Civ. Stor. Nat. Genova, 40, p. 555; 1908, Zeitschr. Wiss. Insektenbiol., 4, p. 304. Bezzi, 1916, Riv. di Sci. Nat. "Natura," 7, p. 179. Austen, 1926, Parasitology, 18, pt. 3, p. 359 (♀ type). J. Bequaert, 1943, Psyche, 49, (for 1942), p. 112 (♀ ♂).

Brachyptomyia fimbriata Speiser, 1907, Ent. News, 18, p. 104.

Brachyptomyia fimbriata Aldrich, 1907, Jl. New York Ent. Soc., 15, p. 6.

Myiophthiria fimbriata Ferris, 1928, Pan-Pacific Entom., 4, p. 140, figs. 1-2 (♀ ♂. Arizona: Tuba, on *Aëronautes s. saxatilis*).

Brachyptomyia femorata Williston, 1896, Ent. News, 7, p. 185 (♂. Wyoming: on *Aëronautes s. saxatilis*. Present location of type unknown). Bezzi, 1900, Rendic. Ist. Lombardo Sc. Lett., (2), 33, p. 522. Aldrich, 1905, Smithson. Misc. Coll., 46, No. 1444, p. 656.

Distribution and Specimens Examined. UNITED STATES. ARIZONA (recorded by Ferris, 1928): Tuba City, Coconino Co., on *Aëronautes s. saxatilis* (V. Tanner). — COLORADO: without precise locality, on *Aëronautes s. saxatilis* (Joel Allen, May, 1882); Golden, Jefferson Co., on *Aëronautes s. saxatilis* (G. Rohwer). — NEBRASKA: Lincoln, Lancaster Co., on *Tachycineta thalassina lepida*, Aug. 29. — NEW MEXICO (recorded by Waterhouse, 1887): Fort Wingate, McKinley Co., ♀ holotype of *fimbriata* (Brit.Mus.) and 2 ♀ topotypes (? or cotypes, at U.S.N.M.), on *Aëronautes s. saxatilis* (R.W. Shufeldt); El Morro, 40 miles S. of Gallup, McKinley Co. (H.S. Barber). — UTAH: Kanab, Kane Co., on *Aëronautes s. saxatilis* (W.J. Breckenridge). — WYOMING (recorded by Williston, 1896). — Also on *Nephoecetes niger borealis*, without locality (from Osten Sacken Coll. — M.C.Z.).

At present *B. fimbriata* is not known outside the western United States. As the known hosts, *Aëronautes*, *Nephoecetes* and *Tachycineta*, all occur south of the United States boundary, the fly will no doubt be found in Mexico.

Bionomics. *M. fimbriata* has been taken most often on 2 species of swifts (Apodidae): *Aëronautes saxatilis* (5 verified records, on the typical race) and *Nephoecetes niger* (1 verified record, on *N. n. borealis*). Swifts may be regarded as the true breeding hosts. Possibly it breeds also on some of the swallows (Hirundinidae), as suggested by the one record from *Tachycineta thalassina lepida*.

Affinities. It is generally agreed that *A. fimbriata* and *B. femorata* were based on one and the same species. The types of both were taken from the same host. The synonymy was first suggested by Speiser (1900) and definitely recognized by Ferris (1928c).

The following differences between *M. fimbriata* and *M. neotropica* supplement the key. Inner orbit narrower, about as wide as mediovertex; orbital bristles more numerous, in several irregular rows, spread over a wider area, which expands both at upper and lower ends; 2 to 4 vertical bristles in upper corner, which is somewhat set off from remainder of side of face. Postvertex shorter

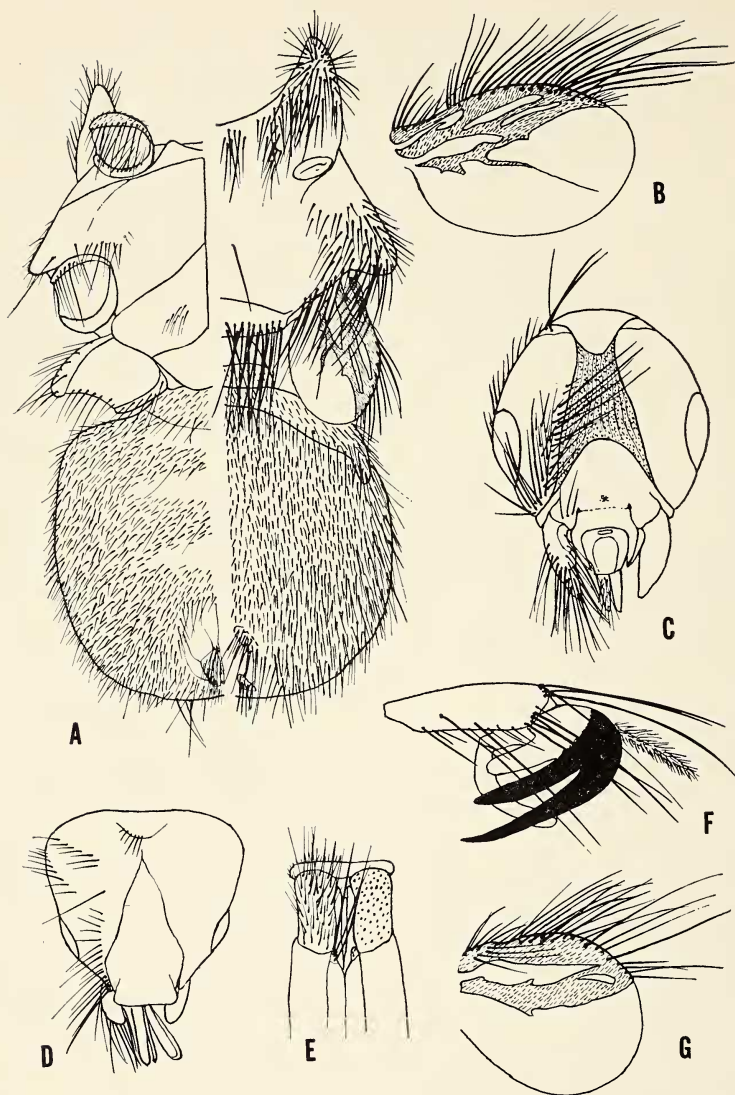


Fig. 35. **A-F**, *Myiophthiria* (*Brachypteromyia*) *fimbriata* (Waterhouse); **A**, **D** and **E**, from Colorado, on *Aëronautes s. saxatilis*; **B**, **C** and **F**, on *Nephoeetes niger borealis*: **A**, thorax and abdomen ventrally and dorsally, ♂; **B**, wing, ♂; **C**, head, ♀; **D**, head ventrally, ♂; **E**, ♂ terminalia; **F**, distitarsus and claw of hind leg, ♂. **G**, *M. (B.) neotropica* J. Bequaert, wing, ♂ holotype, Galipan, on *Aëronautes m. montivagus*.

and broader, more semi-elliptical, much shorter than mediovertex. Eye small, occupying about $\frac{1}{3}$ of upper side of head, seen from above about twice as long as wide, about twice as far from post-vertex as from frons. Antennal appendage longer and narrower, about $2\frac{1}{2}$ times as long as greatest width, widened about mid-length, bluntly rounded at tip. No trace of longitudinal median notal suture anteriorly nor of transverse mesonotal suture. Scutellum slightly longer and narrower; scuto-scutellar suture more arched. Pleurotergal protuberance barely indicated. Wing (Fig. 35B) longer, narrower and more elliptical, about $1\frac{1}{2}$ times as long as wide; rudimentary venation more distinct, very variable (compare Fig. 35B with Ferris, 1928c, p. 141, fig. 2). The posterior sclerites are rudimentary: in the male a pair of very small preapical, dorsal sclerites bear several long bristles; basad of these a transverse group of bristles is set off on each side on a weakly sclerotized, ill-defined area; these sclerotized areas are only indicated in the female by patches of long bristles. Smaller than *M. neotropica*: length from tips of apical arms of frons to hind margin of scutellum, 3.2 to 3.4 mm.; of wing, 1 mm.

Original description of *A. fimbriata*: "Smoky yellow, with the abdomen brown; the epistome pale yellow. The general form and structure are those of *A. pallida*, but it is considerably larger. The antennae are beset with long black erect hairs or setae in front of the eye, continued posteriorly along the orbits of the eyes on each side of the middle opaque disk. This fringe exists, but in a much less degree, in *A. pallida*. The triangle on the vertex is longer than broad, and not transverse as in *A. pallida*. There is a series of black setae along the posterior margin of the head. The thorax is of the same form and with the same black setae as in *A. pallida*, but they are stronger and more conspicuous. The rudimentary wings are pale smoky yellowish, about as long as broad, with numerous black setae on the costal area. The abdomen is somewhat round, clothed with black hair, which is very short on the disk, long at the sides and apex; the base has a transverse arcuate fold; the disk is deeply impressed, but, although this is nearly the same in both examples, it is possibly the result of contraction. The legs are as in *A. pallida*, beset with black hairs. Length 5 lines [10.5 mm.]." The type is a female, now at the British Museum, where I saw it in 1951. According to Dr. G. B. Fairchild (*in litt.*, 1953), the small, triangular wing pad, difficult to measure, is about 1 mm. long.

Original description of *B. femorata*: "Brownish yellow in color, the abdomen, save the basal portion, appearing black beneath the dense black hair. Hair everywhere black and usually long; on the top of the head it forms two long rows, beginning on either side of the base of the antennae and convergent posteriorly. On the sides of the mesonotum it is somewhat tuft-like in front and behind, and forms a long, dense row on the scutellum; the hair of the narrow portion of the abdomen very abundant and shorter; that of the femora rather sparse. The color of the claws, save the basal tooth, is black. Length 6 mm.," Thus far I have been unable to locate the whereabouts of this type, which Williston stated to be a male.

Myiophthiria (Brachypteromyia) neotropica (J. Bequaert)

Figs. 35*G* and 36

Brachypteromyia neotropica J. Bequaert, [1942 (December 31), Bol. Entom. Venezolana, 1, pt. 4, p. 83, *nomen nudum*] 1943 (February), Psyche, 49, (for 1942), pts. 3-4, p. 113, fig. 1 (♂. Venezuela: Galipán, close to Pico del Avila, 2000 m., Distrito Federal, on *Aëronautes m. montivagus*. Type at Mus.Comp.Zoöl., Cambridge, Mass.). Beebe, 1949, Zoologica, New York, 34, pt. 2, p. 61 (Venezuela: Rancho Grande, on *Aëronautes m. montivagus*).

Brachypteromyia neotropica Anduze, Pifano and Vogelsang, 1947, Bol. Entom. Venezolana, Num. Extra, p. 6.

Distribution and Specimens Examined. VENEZUELA (recorded by Beebe, 1949): Galipán, close to Pico del Avila, 2000 m., Distrito Federal, ♂ holotype, on *Aëronautes m. montivagus*; Rancho Grande, between Maracay and Ocumare-de-la-Costa, 3500 ft., State of Aragua, 1 ♂ on *Aëronautes m. montivagus* (W. Beebe).

Original description of *B. neotropica* (revised): *Male*. Head broadly oval, about $1\frac{1}{4}$ times as long (from tips of apical arms of frons to occipital margin) as greatest width. Interocular face at its narrowest nearly 6 times as wide as an eye; inner orbit very wide (near postvertex slightly wider than mediovertex), conspicuously but gradually narrowed downward, the inner margins strongly diverging toward frons; orbital bristles in 2 or 3 irregular rows, crowded in a narrow strip near inner margin and extending over anterior $\frac{3}{4}$ of inner orbit; a fringe of long bristles at edge of outer orbit, near and behind eye; 6 or 7 vertical bristles in upper corner of each inner orbit. Postvertex slightly shorter than mediovertex, flat, triangular with obtuse and ogival lower angle and laterally produced upper corners; occipital margin nearly straight; surface smooth, without rudimentary ocelli, pits or depressions. Frons long and broad, slightly shorter than its distance from occipital margin; suture between interantennal area and lunula superficial; interantennal area very broad and short at base, the apical arms short, enclosing a broad but shallow inward curve; lunula with a minute and shallow median pit close to interantennal suture. Mediovertex well developed, much broader anteriorly, with wide antero-lateral extensions separating genae from lunula. Eye small, nearly elliptical, occupying a little over $\frac{1}{3}$ of upper side of head, seen from above about twice as long as wide, nearly twice as far from postvertex as from frons. Palpi about as long as frons, but as a rule mostly retracted within the rostrum membrane. Antennae medium-sized: 1st segment fused with lunula, bearing 3 to 6 long setae in inner anterior corner; appendage of 2nd segment nearly twice as long as wide, flat, broadly rounded at apex, densely

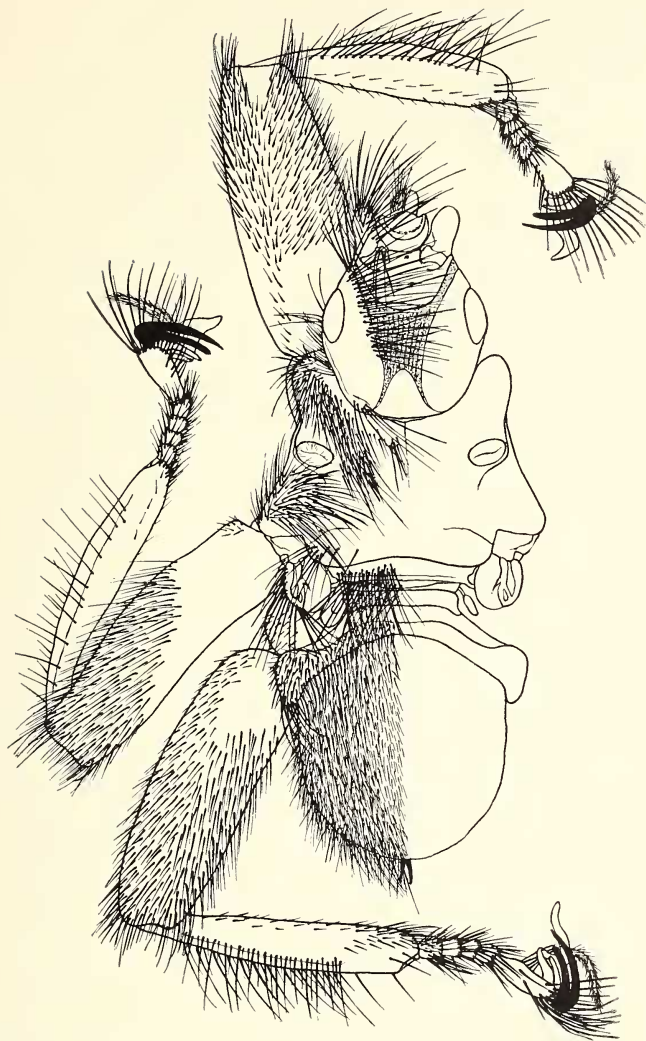


Fig. 36. *Myiophthiria* (*Brachypteromyia*) *neotropica* J. Bequaert, ♂ holotype, Galipan, on *Aëronautes m. montivagus*. × about 10.

covered with many long bristles; arista of 3rd segment protruding beneath appendage of 2nd, much flattened, elongate racket-shaped. Head beneath, on latero-anterior areas (corresponding to the parafacialia and facialia) with many long bristles (vibrissae) in several rows, crowded along inner (buccal) margin; latero-posterior areas (postgenae) with 2 long setae on each side. Thorax wider before wings than long from tip of humeral callosity to base of abdomen; anterior margin of prescutum deeply, but broadly and evenly curved inward. Humeral callosity wide throughout, lobular, broadly rounded at tip, separated by a shallow inward curve from the more prominent prealar angle. Pro-mesonotal suture distinct, but in dorsal view visible only medially behind occipital margin; scuto-scutellar suture deep, straight; a distinct suture between notopleuron and epipleurites at base of wing; posthumeral suture marked at sides only, behind and close to spiracles, curved backward; transverse mesonotal suture placed far back and weakly marked only over lateral third; notal suture weakly indicated over anterior half of mesonotum; other dorsal sutures obsolete, the humeral callosities, notopleura, and anepisterna fused with prescutum. Scutellum very wide and short, with nearly parallel anterior and posterior margins, with a superficial, transverse, preapical, linear groove. Metapleuron with a short, conical, blunt pleurotergal protuberance, covered by the wing. Prothoracic spiracle very large, entirely dorsal; metathoracic spiracle large. Chaetotaxy of thorax consisting of patches of long bristles, difficult to homologize with the muscoid pattern: a dense oblique patch on the humeral callosity extends to beyond spiracle, where it ends far from middle of mesoscutum, but stretches across it some distance from anterior margin; a dense patch over most of anepisternum; 6 or 7 long bristles (postalars) close to wing, on each side behind the transverse mesonotal suture, and more medially a row of 3 bristles (prescutellars); many long scutellars in 2 or 3 irregular rows on disk and a row of similar bristles on hind slope of scutellum. Sternum (Fig. 36): basisternum of prothorax divided by a deep, triangular notch into two broad lobes, bluntly rounded at apex, bare; mesosternum broader than long, with a longitudinal furca, bare except for a narrow patch of setae on each side before mid coxa; basisternum of metathorax with a longitudinal furca ending posteriorly in a deep pit, bearing only a narrow cross-patch of setae (broadly interrupted medially) near hind margin; furcasternum of metathorax deeply depressed medially, saddle-like, bare. Legs very long and stout; fore and mid pairs about alike, hind pair slightly

longer. Coxae short, with many short setae and several long bristles. Trochanters short, with a few short setae near apex. Femora fairly evenly swollen throughout, mostly bare ventrally, dorsally with many stiff hairs and bristles leaving bare a broad basal area (more extensive on mid and less so on hind pair). Tibiae flattened, dorsally with a superficial longitudinal groove bearing a row of erect bristles; a similar row of bristles near outer lower edge; a few short setae elsewhere; apices ventrally with a patch of strong bristles, but without spurs proper. Tarsi: segments 1 to 4 with many short, stiff bristles; distitarsus longer and broader, with very long setae, mostly in a transverse dorsal row at apex. Claws as usual in the genus. Wing (Fig. 35G) very short, pad-like, about twice as long as scutellum, scarcely longer than wide; venation decidedly more reduced than in *B. fimbriata*, crowded in anterior or outer half, of 2 or 3 thick longitudinal veins; costa very thick, with many long bristles on basal $\frac{2}{3}$ and at apex; other veins bare; membrane bare. Halteres well developed, on long stalks. Abdomen (in dried, contracted condition) short, densely hairy both above and below. Dorsally, a short, moderately broad basal tergite, covered with minute setae; behind this a much wider sclerotized tergite, with incurved hind margin and broad side lobes, covered with short, stiff setae, with a row of long bristles at hind margin and a patch of even stronger ones at tips of side lobes. A short, setulose basal sternite. No other sclerotized tergal or sternal plates on the membranous abdomen. Penis valves straight, slender, rod-like, very gradually widened toward base, blunt at apex. Total length, in dried condition, 9 mm.; from tips of apical arms of frons to hind margin of scutellum, 5.6 mm.; of wing, 0.8 mm. Beebe (1949) noted that the abdomen was "bright sage-green" in life. *Female* unknown.

Ornithoetona Speiser, 1902

Ornithoetona Speiser, 1902, Termész. Füzetek, 25, p. 328 (type by original designation: *Ornithomyia erythrocephala* Leach, 1817).

Ornithoetona Patton and Cragg, 1913, Textbook Medical Entomology, p. 407 (error for *Ornithoetona*).

Generic Characters. Fully-winged parasites of birds, not metallic-greenish, often with a dull-green pigment in the haemolymph visible in life through the integument. Head transversely elliptical, deeply inserted between the humeral callosities; occipital margin covering anterior margin of prescutum. Ocelli well developed. Eyes large, occupying most of sides of head, with many

minute ommatidia. Postvertex and frons far apart; soft mediovertex much longer than either. Occipital margin straight or slightly arched. Lunula with a median fovea (sometimes reaching ptilinal suture), superficially divided from the very narrow interantennal area; the latter long, ending in a narrow and shallow, concave emargination, the apical arms short, narrow, slightly diverging (covered by inner margins of antennal appendages). Antennae very wide and long: 1st segment usually with 1 or 2 short setae, rarely bare, either superficially divided from or almost completely fused with lunula, the suture present at least at extreme inner and outer sides as short depressions, that at the inner (median) side often forming a deep fovea (one on each side of the narrow interantennal area); 2nd segment consisting mostly of the long, broad, leaf-like appendage, varying in shape with the species and to some extent also intraspecifically, its upper surface flat, with an oblique, blunt ridge and more or less raised or thickened rims; both appendages parallel, directed forward, covering apical arms of frons and palpi; arista ending in a racket-shaped, translucent plate. Palpi very short, broad. Thorax (Figs. 84, 94 and 104) depressed, much wider than long. Pronotum short, not visible from above. Humeral callosities large, produced forward as prominent, obtusely pointed lobes; posthumeral suture deep at side, curved forward far from median notal suture, not reaching anterior margin; prothoracic spiracle large, near outer hind margin of callosity. Anterior margin of prescutum nearly straight, curving gradually at the side into the inner margin of humeral callosity; transverse mesonotal suture deep, slightly wavy, broadly interrupted medially, at about hind third of mesonotum; anterior ridge of parascutellum fused with mesoscutum; median notal suture very fine, complete from near anterior margin to scutellum; notopleuron well set off throughout from prescutum, wedge-shaped, narrow anteriorly, much broader posteriorly. Dorsal portion of anepisternum broad, lathe-shaped, parallel-sided, with broadly rounded, slightly projecting outer hind edge. Scutellum broad, short, transversely elliptical; hind margin slightly and evenly convex; disk smooth, flat or convex, with or without longitudinal depression or groove; scuto-scutellar suture mostly deep. Pleurotergite of metathorax low, scarcely swollen, without process. Basisternum of prothorax separated from mesosternum by a complete suture, consisting almost entirely of two long, bluntly conical, intercoxal lobes, produced forward and separated by a deep, triangular emargination. Mesosternum divided into basisternum and

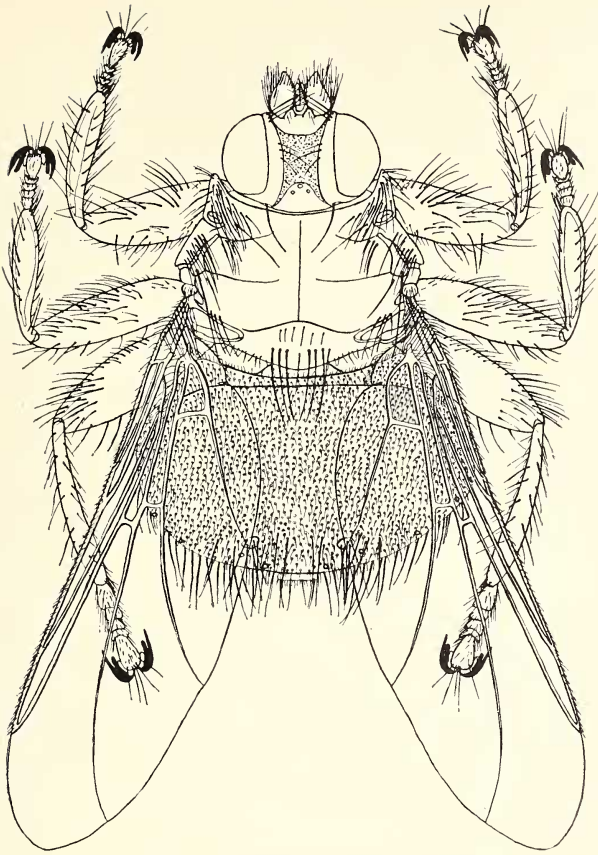


Fig. 37. *Ornithoetona erythrocephala* (Leach), ♀, St. Vincent, on *Amazona guildingii*. $\times$ about 10.

furcasternum by a complete, broadly V-shaped suture (with blunt forward angle). Metasternum undivided, produced forward as a sharp triangle; no metasternal spur near hind coxa. Median longitudinal sternal suture very fine, running over entire mesosternum. Metathoracic spiracle placed below and close to pleurotergite, a short distance from hind coxa. Legs robust; femora usually swollen; tibiae much flattened; hind basitarsus in most species with a transverse basal comb of short, often spine-like setae beneath; tips of tibiae normal in most species, in the Oriental *O. plicata* (v. Olfers) that of fore leg produced as a plate in ♀ and with a tuft of setae in ♂; tibial spurs usually not differentiated

from apical bristles. Claw proper divided to near base in two teeth, the terminal one very long, slender and sharp, the inner one shorter, broader and blunter; in addition a shorter, broad, flattened, bluntly pointed, basal "heel" (claw seemingly tridentate). Wing large, with the complete venation of *Ornithomyia*, including 3 cross-veins; axillary cell rarely with a rudimentary extra longitudinal vein; anterior basal cross-vein at or a short distance basad of anterior cross-vein; 2nd basal at least twice as long as anal cell, not or slightly shorter than 1st basal; 1st, 2nd and 3rd longitudinal veins ending in costa at sharp angles; subcosta complete, ending in costa a little basad of 1st longitudinal; small bullae in anterior basal cross-vein and in basal elbow of 4th longitudinal; posterior basal cross-vein very slanting, upper outer angle of anal cell acute; costa and basicosta setulose; all other veins bare; membrane either completely bare or in some species with a few patches of microtrichia apically; alula very large; calypteres (Fig. 13D) distinct, though reduced in size, the lower one slightly larger than the upper. Abdomen dorsally with the usual fused basal pleurotergites and a pair of preapical sclerites, which are larger in ♂ than in ♀; remainder of dorsum membranous, without striated median area; other median sclerites small or absent in ♀, always present and large in ♂. Seven pairs of abdominal spiracles in membranous sides of abdomen, the 2nd ventral, the 3rd to 7th dorso-lateral, the 6th close to, but not within, the preapical sclerites (Figs. 44C-D). Body more setose than usual on antennae, sides of thorax and abdomen, but middle of notum and sternum nearly bare; orbital bristles few, in one row; usually 1 vertical bristle on each side, close to postvertex. Thoracic bristles as shown in Figs. 8A, 9A and 10A: many, very stiff humerals; small groups of presuturals and postalars; usually 2 notopleurals; 1 supraalar; 1 posterior dorso-central; a few spaced scutellars in one preapical row; hind margin of scutellum with a loose fringe of soft setae; metathoracic pleurotergite bare; a small group of hypopleurals above hind coxa. Abdomen fairly uniformly covered with short setae on small knobs and with many longer bristles behind, both dorsally and ventrally. Abdomen of ♂ ventrally with a median, preapical pair of more or less sclerotized plates; apicad of these, terminalia (Figs. 38D-E) greatly simplified, much as in *Ornithomyia*: gonocoxites (paralobes) reduced to a pair of very small, narrow, conical lobes (with 1 or 2 long setae), one at inner hind corner of each of the lateral areas which extend behind the horseshoe-shaped sclerite; a pair of very heavy, bluntly pointed penis valves (parameres), in side view

with a broad, triangular base; penis rod-like, heavy, moderately pointed.

The genus contains some of the largest hippoboscids known and the largest New World species (*Ornithoetona nitens*).

Ornithomyia nitens Bigot, the type of *Ornithopertha* Speiser, agrees with the other *Ornithoetona* in essential characters; but the antennal appendage is unusually long, parallel-sided and very broadly rounded-truncate at apex, merely exaggerating the characteristic feature of *Ornithoetona*. Moreover, the antennal appendage of *O. orizabae* is somewhat transitional between that of *nitens* and of *erythrocephala*. *Ornithopertha* is here given subgeneric status, but it might well be sunk as a synonym.

The antennal appendage, or enlarged apical extension of the 2nd segment, one of the exclusive features of all Hippoboscidae (Part I, pp. 25-27), is no doubt a refined adaptation to parasitic life in plumage. It allows for swift motion among the feathers, protects the sensoria of the 3rd segment and arista against mechanical injury and dirt, and guides the fly by means of its tactile bristles in the dark recesses of the plumage. This structure reaches its extreme development in *Ornithoetona* and *Stilbometopa*: it becomes very long and wide, is flattened or partly concave, leaf-like, and has a pointed or bluntly rounded tip. Its overdevelopment or hypertely culminates in the weird, shovel-shaped antenna of *O. (Ornithopertha) nitens*. It is questionable whether such extreme development adds materially to the usefulness. As often happens for hypertelic structures, the shape of the leaf-like appendage is subject to much intraspecific variation, which complicates the definition of species in *Ornithoetona*.

Ornithoetona occurs in both the Old and the New World. In the Old World it is restricted to the tropics, being unknown in the Palearctic Region, but common in Africa, southern Asia, Indo-Malaya and Queensland, and accidental only in the temperate parts of Australia. In the New World it is also essentially tropical, but the two common species spread, at least during the summer months, to the eastern half of temperate North America as far as southern Canada (northmost record in 56° N., for *O. erythrocephala*). I recognize only 9 valid species, 5 of which are endemic in the New World.

The puparium, described only for *O. fusciventris*, agrees in general shape, structure of the respiratory apparatus and surface sculpture with that of *Ornithomyia*.

ENTOMOLOGICA AMERICANA

Key to American Species of *Ornithoctona*

1. Antennal appendage about $\frac{2}{3}$ of height of head, over 3 times as long as its greatest width, spoon-shaped, with nearly parallel sides and broadly rounded tip, the upper surface deeply and broadly grooved basally. Interocular face at post-vertex slightly wider than an eye in ♀, distinctly narrowed below. Upper orbit shorter than width of inner orbit at ptilinal suture. Abdomen of ♀ without median dorsal sclerites. Apical portion of wing (beyond tip of costa) with small patches of microtrichia. Wing 11 to 12.5 mm. long *O. nitens*
- Antennal appendage at most 3 times as long as its greatest width, less than $\frac{2}{3}$ of height of head, the sides not parallel throughout, with narrowed, either pointed or blunt tip..... 2
2. Upper orbit shorter than width of inner orbit at ptilinal suture. Anterior ocellus below a line drawn along upper eye margins; posterior ocelli on or close to this line 3
- Upper orbit fully as long as width of inner orbit at ptilinal suture. Anterior ocellus placed on or slightly above a line drawn along upper eye margins; posterior ocelli well above this line. Upper surface of antennal appendage grooved lengthwise, except at tip. Abdomen in both sexes with 3 median dorsal sclerites. Apical third of wing partly covered with microtrichia 4
3. Antennal appendage nearly twice as long as its greatest width or shorter, with at least the inner margin convexly curved in basal half, more or less pointed at tip, the edges of the apical portion somewhat upturned. Interocular face less than twice as long as wide, at its narrowest wider than an eye in both sexes. Median tergal sclerites of abdomen present and large in ♂, absent in ♀. Wing entirely bare. Wing 7 to 8 mm. long in ♂, 8.5 to 10 mm. in ♀ *O. erythrocephala*
- Antennal appendage nearly three times as long as its greatest width, almost parallel-sided basally, gradually narrowed and triangular apically, with blunt tip, the basal upper surface superficially grooved. Interocular face more than twice as long as wide, at its narrowest distinctly narrower than an eye in ♂. Apical portion of wing partly covered with microtrichia. Wing 10 mm. long. (♀ unknown) *O. orizabae*

4. Larger, the wing 8.5 to 9.5 mm. long. Antennal appendage fully two and one-half times as long as its greatest width; the pointed tip long and narrow seen from above, compressed from the sides. Scutellum with 3 or 4 pairs of strong preapical setae *O. oxycera*
- Smaller, the wing 5.5 to 7 mm. long. Antennal appendage nearly twice as long as its greatest width, gradually widened basally, the outer and inner margins about equally curved; the short tip either rounded or bluntly pointed, not compressed from the sides. Scutellum with 2 or 3 pairs of rather weak preapical setae *O. fusciventris*

Subgenus *Ornithoctona*, proper

Antennal appendage 2 to 3 times as long as its greatest width, more or less tapering apically; outer and inner margins usually curved outwardly, seldom nearly parallel basally; tip distinctly narrowed, either sharply pointed or bluntly rounded.

Ornithoctona erythrocephala (Leach)

Figs. 8A, 9A, 10A, 13D, 37, and 38A-K

Ornithomyia erythrocephala Leach, 1817, Gen. Spec. Eproboscideous Ins., p. 13; Pl. 27, figs. 4-6 [1818, Mem. Werner. Nat. Hist. Soc., Edinburgh, 2, pt. 2, p. 559; Pl. 27, figs. 4-6] (no sex; no host. Brazil. Type ♀ at Brit. Mus.). Wiedemann, 1830, Aussereurop. Zweifl. Ins., 2, p. 610 (copy of description). Walker, 1849, List Dipt. Brit. Mus., 4, p. 1143 (Jamaica: on *Corvus jamaicensis*, *Columba "rufina"* [*C. leucocephala*], "*Tityra leuconotus*" [*Platypsaris niger*], "*Geotrygon montana*" [*Oreopeleia m. montana*], *Geotrygon "sylvatica"* [*G. versicolor*], "*Turtur leucopterus*" [*Zenaida a. asiatica*], "*Ephialtes grammicus*" [*Pseudoscops grammicus*], *Sauvothera v. vetula*, "*Herodias virescens*" [*Butorides virescens maculatus*], *Falco c. columbarius*, "*Peristera jamaicensis*" [*Leptotila j. jamaicensis*], "*Strix pratincola*" [*Tyto alba furcata*], and "*Zenaida amabilis*" [*Z. aurita zenaida*]. Brazil. Peru. Venezuela). Osten Sacken, 1858, Cat. Dipt. North America, p. 86; 1878, Smithson. Misc. Coll., No. 270, p. 213 (Cuba: Canada: Quebec). van der Wulp, 1883, Tijdschr. v. Entom., 26, p. 59 (Guadeloupe). Gundlach, 1887, An. Soc. Españ. Hist. Nat., 16, p. 199. Johnson, 1894, Proc. Ac. Nat. Sci., Philadelphia, p. 281. Williston, 1896, Trans. Ent. Soc. London, p. 439 (St. Vincent). Coquillett, 1900, Proc. U. S. Nat. Mus., 22, p. 269 (Puerto Rico: Adjuntas, on *Falco sparverius loquaculus*; *Culebra* I.).

Ornithomyia (*Ornithoctona*) *erythrocephala* Austen, 1903, Ann. Mag. Nat. Hist., (7), 12, p. 263 (type).

Ornithoctona erythrocephala Speiser, 1902, Termész. Füzetek, 25, p. 329; 1904, Zeitschr. Syst. Hym. Dipt., 4, p. 82 (synonymizes type of *gemina* Thomson); 1904, Ann. Mus. Civ. Stor. Nat. Genova, 41, p. 345. Washburn, 1905, Univ. Minnesota, Agric. Expt. Sta. Bull. 93, p. 163 (Minnesota: on *Buteo p. platypterus*). Aldrich, 1905, Smithson. Misc. Coll., 46, No. 1444, p. 654 (Guadeloupe). Speiser, 1907, Ent. News, 18, p. 103; 1908, Zeitschr. Wiss. Insektenbiol., 4, pp. 303 and 304. Newstead, 1909, Ann. Trop.

Med. Paras., 3, p. 467 (Jamaica: Worthy Park, on "*Conurus nanus*" [*Aratinga nana*]; Friendship, Sa. Cruz Valley, St. Elizabeth, on "*Falco peregrinus nigriceps*" [*F. peregrinus anatum*]); 1910, Bull. Dept. Agric., Jamaica, (N. S.), 1, pt. 3, p. 175 (same records). Johnson, 1913, Bull. Amer. Mus. Nat. Hist., 32, p. 90 (Florida: St. Augustine). Lutz, Neiva and da Costa Lima, 1915, Mem. Inst. Osw. Cruz, 7, pp. 186 and 188; Pl. 28, fig. 8 (Brazil: São Paulo; Florianopolis, State Sa. Catharina, supposedly on "*Catharista atrata*" [*Coragyps atratus foetens*]). Brêthes, 1920, An. Soc. Cientif. Argentina, 89, p. 33 (Peru: Lima). Johnson, 1922, Psyche, 29, p. 84 (Quebec: Metis, on *Falco c. columbarius*; Montreal, on *Botaurus lentiginosus*. Cuba: on "*Buteo borealis*" [*B. jamaicensis umbrinus*] and *B. platypterus cubanensis*; Holguin, on "*Geotrygon montana*" [*Oreopeleia m. montana*]. Puerto Rico, on *Falco sparverius loquaculus*³⁵). Bau, 1922, Centralbl. Bakt. Parasit., Abt. 2, 57, p. 276. Wolcott, 1924, Jl. Agric. Univ. Puerto Rico, 7, (for 1923), pt. 1, p. 234 (Puerto Rico: Aibonito and Cabo Rojo, on "sparrow hawk" [*Falco sparverius loquaculus*]; Caguas, on "Porto Rico dove" [*Columbigallina passerina portoricensis*]). Johnson, 1925, Occ. Papers Boston Soc. Nat. Hist., 7, p. 293 (Maine); 1925, Bull. Northeastern Bird-Banding Assoc., 1, pt. 4, p. 52 (Canadian records repeated). Bau, 1929, Zoolog. Anzeiger, 85, p. 11 (Mexico. Cuba. Venezuela. Brazil: Rio Grande do Sul. One of these specimens on "*Gymnoglaux* sp.'). Faleoz, 1930, Encyclop. Entom., Ser. B, Diptera, 5, (for 1929), p. 38 (Costa Rica. Mexico. Peru: Lima. Colombia, on domestic pigeon. Chile: Valparaiso. Brazil: Guaratuba, State Paraná; Rio Grande do Sul. Argentina: Chaco de Santiago, at the Rio Salado. ♀ ♂. Synonymizes *gemina* Thomson, *bellardiana* Rondani, *haitiensis* Bigot and *robusta* van der Wulp). J. Bequaert, 1933, Rev. Chilena Hist. Nat., 37, p. 163. Wolcott, 1936, Jl. Agric. Univ. Puerto Rico, 20, pt. 1, p. 392 (Puerto Rico: Lajas; Las Marias, on "West Indian red-tailed hawk" [*Buteo j. jamaicensis*]). Spencer, 1938, Proc. Ent. Soc. British Columbia, 34, p. 44 (British Columbia: Osoyoos, on *Falco peregrinus anatum*). Strickland, 1938, Canad. Jl. Res., Sect. D, 16, p. 219 (Alberta: on "burrowing hawk" [for broad-winged hawk, *Buteo p. platypterus*]). Brimley, 1938, Insects North Carolina, p. 389 (North Carolina: Raleigh, on "broad-winged hawk" [*Buteo p. platypterus*]; Charlotte, on "Cooper's hawk" [*Accipiter cooperii*]). J. Bequaert, 1939, Science, 89, p. 268; 1940, Mem. Soc. Cubana Hist. Nat., 14, No. 4, p. 315; 1940, Rev. Acad. Colombiana Cienc. Ex. Fis. Nat., 3, No. 12, p. 415. Wolcott, 1941, Jl. Agric. Univ. Puerto Rico, 25, pt. 1, p. 121 (Puerto Rico: on "*Gymnasio nudipes*" [*Otus n. nudipes*]; Mayaguez, on "*Buteo borealis*" [*Buteo j. jamaicensis*]). J. Bequaert, 1942, Bol. Entom. Venezolana, 1, pt. 4, p. 80; 1943, Jl. of Parasitology, 29, p. 135. Stuardo, 1946, Catálogo Dípteros Chile, p. 187. Anduze, Pifano and Vogelsang, 1947, Bol. Entom. Venezolana, Num. Extra, p. 6. Beatty, 1947, Jl. Agric. Univ. Puerto Rico, 28, (for 1944), pts. 3-4, p. 154 (St. Croix: on *Buteo j. jamaicensis*). MacArthur, 1948, Bull. Publ. Mus. Milwaukee, 8, pt. 4, pp. 403 and 405, figs. 240-241 (Illinois: without precise locality, on *Falco s. sparverius*; Niles, on *Buteo p. platypterus*; Calumet Lake, on *Accipiter cooperii*; Havana. Minnesota: without precise locality, on *Buteo p. platypterus*; Ortonville, Big Stone Co., on *Buteo p. platypterus*. Wisconsin: without precise locality). Thompson, 1949, Ent. Mo. Mag., 85, p. 248 (Jamaica: Spring Gardens, Portland, on *Buteo j. jamaicensis*; Mt. James, St. Andrew, on *Buteo j. jamaicensis*; Cross Roads, St. Andrew, on *Buteo j. jamaicensis*; Kew

³⁵ The record from Dominica, on *Nyctanassa violacea*, is erroneous, as the specimen was collected in Jamaica.

- Park, Westmoreland, on *Pseudoscops grammicus*; Hermitage, St. Andrew, on *Oreopeleia m. montana*; Bath, St. Thomas, on *Chordeiles minor gundlachi*). Herms, 1950, Medical Entomology, 4th Ed., p. 414. Wolcott, 1951, Jl. Agric. Univ. Puerto Rico, **32**, (for 1948), pt. 3, p. 530. J. Bequaert, 1951, Agricultura Técnica, Santiago de Chile, **10**, pt. 1, (for 1950), p. 8. Schuurmans Stekhoven, 1952, Beiträge zur Fauna Perus, **3**, Wissenschaftl. Bearbeit., pp. 94 and 101.
- Ornithomyia cryptocephala* Stahl, 1882, Fauna Puerto Rico, **2**, p. 206 (Puerto Rico. Error for *erythrocephala*).
- Ornithoctena erythrocephala* Gowdey, 1926, Dept. Agric. Jamaica, Ent. Bull., **4**, pts. 1-2, p. 89 (error for *erythrocephala*).
- Ornithomyia nebulosa* Say, 1823, Jl. Ac. Nat. Sci. Philadelphia, **3**, p. 102 (no sex. United States, without precise locality, on *Strix nebulosa*. Type lost). Wiedemann, 1830, Aussereurop. Zweifl. Ins., **2**, p. 610 (locality surmised to be Pennsylvania). Say, 1837, Oeuvres Entomologiques, edit. by Gory, p. 103. Walker, 1849, List Dipt. Brit. Mus., **4**, p. 1143. Osten Sacken, 1858, Cat. Dipt. North America, p. 86. Say, 1859, Complete Writings, edit. by LeConte, **2**, p. 87. Osten Sacken, 1878, Smithson. Misc. Coll., No. **270**, p. 213. Brodie and White, 1883, Check List Ins. Dom. Canada, p. 57. Aldrich, 1905, Smithson. Misc. Coll., **46**, No. 1444, p. 654.
- Ornithomyia nebulosa* Howard, 1883, South Carolina, Resources and Population, p. 275.
- Ornithoctena* (?) *nebulosa* Speiser, 1907, Ent. News, **18**, p. 103; 1908, Zeitschr. Wiss. Insektenbiol., **4**, p. 303.
- Ornithoctena nebulosa* Peters, 1936, Bird-Banding, **7**, p. 14 (Maryland: on *Falco c. columbarius*).
- Ornithomyia gemina* Thomson, 1869, Svensk. Freg. Eugenies Resa, Vet. Iakttag., **2**, Zool., pt. 1, Insekter, Häft 12, (1868), p. 611 (♀; no host. Peru: Callao. Type at Stockholm Mus.).
- Ornithomyia bellardiana* Rondani, 1878, Ann. Mus. Civ. Stor. Nat. Genova, **12**, p. 157 (no sex; no host. Mexico. Supposed ♀ type at Genoa Mus., now labelled "*Ornithomyia pyrrocephala*").
- Ornithoctena bellardiana* Speiser, 1902, Termész. Füzetek, **25**, p. 329; 1904, Ann. Mus. Civ. Stor. Nat. Genova, **41**, pp. 344 (type) and 345. Aldrich, 1905, Smithson. Misc. Coll., **46**, No. 1444, p. 654. Speiser, 1907, Ent. News, **18**, p. 103; 1908, Zeitschr. Wiss. Insektenbiol., **4**, p. 304. Bau, 1922, Centralbl. Bakt. Parasit., Abt. **2**, **57**, p. 276; 1929, Zoolog. Anzeiger, **85**, p. 11 ("San Francisco, Cuba").
- Ornithomyia pyrrocephala* "Rondani" Speiser, 1904, Ann. Mus. Civ. Stor. Nat. Genova, **41**, p. 344 (no sex; no host. Mexico. On the label of the presumed type of *O. bellardiana*, which is not now at the Genoa Mus. under that name; with new description).
- Ornithomyia haitiensis* Bigot, 1885, Ann. Soc. Ent. France, (6), **5**, p. 242 (no sex; no host. Haiti. Type from Bigot Coll., now in J.E. Collin Coll.). Lutz, Neiva and da Costa Lima, 1915, Mem. Inst. Osw. Cruz, **7**, p. 192 (copy of description).
- Ornithoctena haitiensis* Speiser, 1902, Zeitschr. Syst. Hym. Dipt., **2**, p. 168 (type; redescribed); 1904, Ann. Mus. Civ. Stor. Nat. Genova, **41**, p. 345. Bau, 1922, Centralbl. Bakt. Parasit., Abt. **2**, **57**, pp. 274 and 276 (Cuba: on "Kampfhahn"; [probably a domestic "fighting cock"]).
- Ornithoctena haitiensis* Aldrich, 1905, Smithson. Misc. Coll., **46**, No. 1444, p. 654 (also misspelled *hatisensis* on same page). Speiser, 1907, Ent. News, **18**, p. 103; 1908, Zeitschr. Wiss. Insektenbiol., **4**, p. 304.
- Ornithomyia robusta* van der Wulp, 1903, Biol. Centr.-Amer., Diptera, **2**, p. 431; Pl. 13, figs. 5 and 5a-c (♀ ♂ according to the author; but all types ♀, according to Austen, 1903; no host. Mexico: Jalapa. Guatemala: Zapote. Costa Rica: Caché, ♀ now labelled as type. Panama: Volcan de

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- Chiriqui. Cotypes ♀ at Brit.Mus.). Austen, 1903, Ann. Mag. Nat. Hist., (7), 12, p. 262 (types all ♀; synonymized with *erythrocephala* Leach).
- Ornithoctona robusta* J. Bequaert, 1938, Carnegie Publ. No. 499, p. 227.
- Ornithomyia buteonis* Swenk, 1916, Jl. New York Ent. Soc., 24, p. 133 (no sex. Nebraska: Neligh, holotype, on "broad-winged hawk" [*Buteo p. platypterus*]. Costa Rica: Guápiles, paratype, without host. Types, both ♀, at Dept. Entom., Univ. Nebraska, Lincoln). Muma, 1952, Bull. Univ. Nebraska State Mus., 3, pt. 3, p. 14 (holotype only listed).
- Ornithomyia costaricensis* Swenk, 1916, Jl. New York Ent. Soc., 24, p. 134 (no sex; no host. Costa Rica: Juan Viñas. Type ♀ at Dept. Entom., Univ. Nebraska, Lincoln). Muma, 1952, Bull. Univ. Nebraska State Mus., 3, pt. 3, p. 14 (type).
- Ornithoctona albiventris* Bau, 1922, Centralbl. Bakt. Parasit., Abt. 2, 57, pp. 274 and 276 (♀. Cuba: Estación Meyer, Prov. Sa. Clara, on "Grosse weisse Nachteule," surmised by Bau to have been "*Strix flammea* var. *furcata* Ridg." [*Tyto alba furcata*]. Type at Berlin Mus.).

Distribution and Specimens Examined. DOMINION OF CANADA. ALBERTA (recorded by Strickland, 1938): Belvedere, on *Buteo p. platypterus* (C.G. Harrold). — BRITISH COLUMBIA (recorded by Spencer, 1938): Okanagan Falls, on *Falco peregrinus anatum* (K. Racey; R.A. Cumming and G.J. Spencer). — MANITOBA: Vivian, on *Buteo p. platypterus* (A.H. Short); Winnipeg, on *Buteo p. platypterus* (J.O. Soper). — NOVA SCOTIA: Cape North, on chicken hawk (T. McElvoy). — ONTARIO: Macdiarmid, Lake Nipigon, on *Buteo p. platypterus* (N.K. Bigelow); 20 miles N.E. of Nipigon, on *Buteo p. platypterus* (A.E. Allin); Spring Bay, Manitoulin, on *Buteo p. platypterus* (J.L. Baillie); Point Pelée, on hawk (A.W. Andrews); Schreiber, on *Buteo jamaicensis borealis* (Peterson and Muir); Fort Severn, 56° N. (C.E. Hope). — QUEBEC (recorded by Osten Sacken, 1878; Johnson, 1922): Little Metis, on *Falco c. columbarius* (L.M. Terrill); Montreal, on *Botaurus lentiginosus* (J. Ouellet); Maisonneuve, on *Pandion haliaetus carolinensis* (Frère Roger Albert); Kamouraska (au Moulin), Kamouraska Co., on *Pandion haliaetus carolinensis* (W. LaBrie); Val d'Espoir, on *Falco c. columbarius*, June (Frère Adrien Robert).

UNITED STATES. CONNECTICUT: West Haven, New Haven Co., on *Buteo p. platypterus* (R.C. Morrill). — FLORIDA (recorded by Johnson, 1913): St. Augustine, St. Johns Co. (C.W. Johnson). — GEORGIA: Eastanollee, Stephens Co. (D.M. Moore); Stone Mountain, De Kalb Co., on *Falco s. sparverius* (W.E. Bowers); [Macon, Bibb Co., on *Accipiter striatus velox*; Atlanta, Fulton Co. — According to P.W. Fattig, *in litt.*; not seen]. — ILLINOIS (recorded by MacArthur, 1948): Chicago, Oct. 13, on *Falco s. sparverius* (J. Schreiber); Niles, Cook Co., on *Buteo p. platypterus*, Apr. 19 (A.B. Wolcott); Calumet Lake near Chicago, on *Accipiter cooperii*, Apr.

20 (J. Friesser); Havana, Mason Co., Sept. 16 (Hempel). — IOWA: Ames. — KANSAS: Douglas Co. (F.H. Snow); Baldwin City, Douglas Co., June 9 (A.B. Cramlington); Leavenworth, Leavenworth Co., on *Accipiter striatus velox* (M.J. Brumwell). — MAINE (recorded by Johnson, 1925): Orono, Penobscot Co., on *Falco c. columbarius*, May 20 (C.P. Alexander); Lincoln, Penobscot Co., on *Accipiter striatus velox* (A.E. Brower). — MARYLAND (recorded by Peters, 1936): Patuxent Refuge, Bowie, Prince Georges Co., on *Falco c. columbarius*, Apr. 10; Laurel, Prince Georges Co., on *Buteo p. platypterus*, May 11, *Buteo jamaicensis borealis*, March, and *Falco c. columbarius*, May 4 (E.B. Marshall). — MASSACHUSETTS: Hyde Park, Suffolk Co., on *Falco c. columbarius*, May 6; Concord, Middlesex Co., on *Falco c. columbarius* (B.P. Mann); Berlin, Worcester Co. — MICHIGAN: Whitefish Point, Chippewa Co., on *Accipiter striatus velox*, May 22 (J.S. Ligon). — MINNESOTA (recorded by Washburn, 1905; MacArthur, 1948): without precise locality, on *Buteo p. platypterus*, May 1 and 14; Ortonville, Big Stone Co., on *Buteo p. platypterus*. — MISSISSIPPI: Rosedale, Bolivar Co., on *Buteo p. platypterus* (M.D. Vaiden); A. and M. College, Oktibbeha Co. — MISSOURI: Columbia, Boone Co., on hawk (L. Jeffrey). — MONTANA: Kendall, Fergus Co., May 25 (W.L. Knull). — NEBRASKA (recorded by Swenk, 1916, as *O. buteonis*): Neligh, Antelope Co., on *Buteo p. platypterus*, Apr. 26 (holotype of *O. buteonis*. — M. Cary). — NEW HAMPSHIRE: Sandwich, Carroll Co., on *Buteo p. platypterus* (R.G. Carpenter, Jr.). — NEW JERSEY: Stockholm, Sussex Co., on *Accipiter striatus velox* (J. Vonlengerke). — NEW YORK: without precise locality, on *Haliaeetus l. leucocephalus* (J. Akhurst); Orient, Long Island, on *Accipiter striatus velox*, May 16, and *Accipiter cooperii*, Oct. 6 (Roy Latham); Yonkers, Westchester Co., on *Buteo p. platypterus* (I.D. Dobrosky); Stuyvesant Falls, Columbia Co., Sept. 12, on *Buteo jamaicensis borealis*; Bainbridge, Chenango Co., March 18; West Point, Orange Co., on *Buteo p. platypterus*, Apr. 18, Oct. 10, Nov. 16 (W. Robinson); Westport, Essex Co., on *Buteo p. platypterus* (E.J. Gerberg); Albany, on *Phasianus colchicus*, Oct. 17 (A. Paladin). — NORTH CAROLINA (recorded by Brimley, 1938): Raleigh, Wake Co., on *Buteo p. platypterus* (Mrs. R.C. Simpson); Charlotte, Mecklenburg Co., on *Accipiter cooperii* (W. Smith); Washington, Beaufort Co., on (?wild) pigeon (H.C. Bragaw); Swan I., Currituck Sound, Currituck Co., on *Branta c. canadensis* (C.M.B. Cadwallader). — NORTH DAKOTA: Turtle Mts., 6 miles N. W. of St. John, Rolette Co., on *Buteo p. platypterus* (A. Wetmore). — OHIO: South Bass I., Put-in Bay,

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Ottawa Co., on *Phasianus colchicus* (F.J. Ligas); Greenville, Darke Co., on *Megaceryle a. alcyon* (R. Rausch); Ottawa Co., May 22, on *Accipiter cooperii* (E.S. Thomas); Franklin Co., on *Sphyrapicus v. varius* (C.F. Walker). — PENNSYLVANIA: without precise locality, on *Accipiter striatus velox* (L. Luttringer); Berks Co., on *Buteo p. platypterus* (O.G. Harrold); Coburn, Centre Co., on *Accipiter striatus velox* (H.K. Wingard); Dreherstown, Schuylkill Co., on *Accipiter gentilis atricapillus*; Delaware Co., on *Haliaeetus l. leucocephalus* (C.W. Johnson); Meekville, Berks Co., on *Buteo p. platypterus* (L.S. Dillon); Reading, Berks Co., on *Falco c. columbarius* (L.S. Dillon). — WEST VIRGINIA: Fort Spring, Greenbrier Co. (Mrs. W.L. Mitchell). — WISCONSIN (recorded by MacArthur, 1948): Dane Co. (C.A. Herrick).

MEXICO (recorded by Rondani, 1878, as *O. bellardiana*; van der Wulp, 1903, as *O. robusta*; Speiser, 1904, as *O. pyrrhocephala*; Bau, 1929; Falcoz, 1930); without precise locality (Ac.N.S.Phila.), and on *Dactylortyx thoracicus* and *Penelopina nigra* (Esc.N.C. Biol.); Santa Rosa, Comitán, State of Chiapas, on *Cyanolyca pulchra mitrata*, *Pharomachrus m. mocino*, and *Buteo* sp. (Esc.N.C. Biol.); Orizaba, State of Vera Cruz (A. Sallé); Jalapa, State of Vera Cruz (F.D. Godman. — Cotype ♀ of *robusta*).

GUATEMALA (recorded by van der Wulp, 1903, as *O. robusta*): Zapote (G.C. Champion. — Cotype of *robusta*).

REPUBLIC OF HONDURAS: Subirana, on *Buteo magnirostris argutus* and *Zenaida a. asiatica*, Dept. Yoro, about 15° 6' N., 87° 23' W. (R. Stadelman).

NICARAGUA: San Rafael del Norte, on *Herpetotheres c. cachinnans* and *Accipiter erythrocnemius chionogaster* (W.deW. Miller).

COSTA RICA (recorded by van der Wulp, 1903, as *O. robusta*; Swenk, 1916, as *O. buteonis* and *O. costaricensis*; Falcoz, 1930): without precise locality (U.S.N.M.); southwestern section, on *Odontophorus* sp. (C.H. Lankester); Guápiles (paratype ♀ of *buteonis*. — J.C. Crawford); Juan Viñas (holotype ♀ of *costaricensis*. — L. Bruner); Caché (H. Rogers. — ♀ at Brit.Mus. now labelled type of *robusta*).

PANAMA (recorded by van der Wulp, 1903, as *O. robusta*): Volcán de Chiriqui, 9000 ft. (G.C. Champion. — ♀ cotype of *robusta*); Salta, Boquete, Chiriqui Prov., 5800 ft., on *Odontophorus guttatus veraguensis* (G.F. Ferris); Chorrera, Chiriqui Prov., on *Leptotila v. verreauxi* (G.B. Fairchild); Boquete, Chiriqui Prov., on *Leucopternis princeps* (L. Wheeler); El Volcán, Chiriqui Prov., on wild pigeon (C.B. Worth); San José, Pearl Is. (J.P.E. Morri-

son); Barriles, a few miles W. of El Volcán, Chiriqui Prov., on *Buteo jamaicensis costaricensis*, *Odontriorchis palliatus*, and *Myiobius barbatus atricaudus* (Mrs. M.E. McLellan Davidson).

ANTILLES. BAHAMAS: without precise locality (U.S.N.M.). — CUBA (recorded by Osten Sacken, 1878; Bau, 1922 and 1929, as *O. bellardiana*, *O. haitiensis* and *O. albiventris*; Johnson, 1922): without precise locality, on *Zenaida aurita zenaida* (J. Gundlach), *Oreopeleia m. montana* (Brit.Mus.), *Buteo platypterus cubanensis*, *Asio stygius sigaupa* (Hno. Robert), and *Accipiter gundlachi* (G. Aguayo); Guantanamo, Prov. Oriente, on *Oreopeleia chrysia*; Ensenada de Cochinos, Prov. Las Villas (Sa. Clara), on *Zenaida aurita zenaida* (T. Barbour and L.A. Shaw); Santiago de las Vegas, Prov. Habana, on *Glaucidium siju* (S.C. Bruner); Rangel, Prov. Pinar del Río (Brother Chrysozone); Guanajay, Prov. Pinar del Río (Palmer and Riley); Jiguani, Prov. Oriente (T. Barbour and L.A. Shaw); El Guama, Prov. Pinar del Río (Palmer and Riley); Tanamo, Prov. Oriente; Santiago de Cuba, Prov. Oriente, on chicken hawk; Las Animas, Sierra Rangel, Prov. Pinar del Río (Est.Exp.Agr.Cuba); Preston, Prov. Oriente, on *Zenaidura m. macroura* and *Holotris leucocephala gundlachi* (J.L. Peters); San Diego de los Baños, Prov. Pinar del Río, on *Melanerpes s. supercilialis* (Burleigh and Duvall); Holguin, Prov. Oriente, on *Oreopeleia m. montana*; Artemisia, Prov. Pinar del Río, on *Accipiter gundlachi*, *Circus cyaneus hudsonius*, and *Oreopeleia chrysia* (I. Perez Vigueras). — ISLE OF PINES: Los Indios, on *Amazona l. leucocephala* (G. Link). — JAMAICA (recorded by Walker, 1849; Newstead, 1909 and 1910; Thompson, 1949); without precise locality, on *Corvus jamaicensis*, *Columba leucocephala*, *Oreopeleia m. montana*, *Pseudoscops grammicus*, *Zenaida a. asiatica*, *Falco c. columbarius*, *Tyto alba furcata*, *Zenaida aurita zenaida*, *Butorides virescens maculatus*, and *Leptotila j. jamaicensis* (Walker's specimens at Brit.Mus.); Troy, on *Strix* sp. (W.R. Maxon); Mandeville (Elizabeth B. Bryant); Spanish Town, on *Columba leucocephala* (W.D. Neish); Claremont (L. Perkins); Bath, St. Thomas, on *Nyctanassa v. violacea*³⁶ (A.H. Verrill and O. Bangs) and *Chordeiles minor gundlachi* (Swainson); Quickstep, St. Elizabeth, on *Corvus jamaicensis* (C.B. Lewis); Falmouth, on *Buteo j. jamaicensis*, *Siphonorhis a. americanus*, *Columba leucocephala*, *Zenaida aurita zenaida* and *Z. a. asiatica* (H.B. Carroll); Spring Gardens,

³⁶ Johnson's (1922) erroneous record from Dominica was based on this specimen, now at M.C.Z.

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Portland, on *Buteo j. jamaicensis* (G.B. Thompson); Mt. James, St. Andrew, on *Buteo j. jamaicensis* (G.B. Thompson); Hermitage, St. Andrew, 1800 ft., on *Oreopeleia m. montana* (H.B. Tordoff); Hartford near Priest River, on *Buteo j. jamaicensis* (W.R. Maxon); Kew Park, Westmoreland, 1100 ft., on *Pseudoscops grammicus* (H.B. Tordoff); Cross Roads, St. Andrew, on *Buteo j. jamaicensis* (G.B. Thompson). — HISPANIOLA (recorded by Bigot, 1885, as *O. haitiensis*): Constanza, Rep. Dominicana, on *Oreopeleia caniceps leucometopius* (W.L. Abbott); El Río, Rep. Dominicana, on *Buteo j. jamaicensis* and *Temnotrogon roseigaster* (W.L. Abbott); Farabacoa, Rep. Dominicana, on *Amazona ventralis* (A. Wetmore); Sanchez, Rep. Dominicana, on *Zenaida a. asiatica* and *Buteo j. jamaicensis* (A. Wetmore); Moca, Rep. Dominicana, on *Falco* sp. (Juan Lopez, through R. Frey); Puerto Plata, Rep. Dominicana (Hurst); Kenscoff near Petionville, 4500 ft., Haiti, on *Falco sparverius dominicensis* (W.A. Weber); Port-au-Prince, Haiti; Moline, Haiti, on *Falco c. columbarius*; Furey, Haiti, on *Buteo j. jamaicensis* (G.E. Folk); Huiche, Haiti, on *Columba i. inornata* (A. Wetmore). — MONA ISLAND: on *Columba i. inornata* (B.S. Bowdish). — PUERTO RICO (recorded by Stahl, 1882; Coquillett, 1900; Johnson, 1922; Wolcott, 1924, 1936, 1941 and 1951); Adjuntas, on *Otus n. nudipes* (H.E. Anthony) and on *Falco sparverius loquaculus* (C.W. Richmond); Mayaguez, on *Zenaidura m. macroura* and *Buteo j. jamaicensis* (H.L. Dozier), and on *Saurothera vetula vieilloti* (B.S. Bowdish); Las Marias, on *Buteo j. jamaicensis* (S.T. Danforth); Aibonito, on *Falco sparverius loquaculus* (A. Wetmore); Caguas, on *Columbigallina passerina portoricensis*; Salinas, on *Leucophoyx t. thula* (A. Wetmore); Lajas, on *Buteo j. jamaicensis* (S.T. Danforth); Cabo Rojo, on *Falco sparverius loquaculus*; La Parquera, on *Asio flammeus portoricensis* (M. Agraft); El Yunque, on *Buteo platypterus cubanensis*; Rio Rondo, Mayaguez (A.R. Quiles). — ST. CROIX (recorded by Beatty, 1947): on *Buteo j. jamaicensis* (H.A. Beatty). — ST. THOMAS: (R. Sebastien), and in nests of *Zenaida a. aurita* and *Columba leucocephala* (G.A. Seaman). — SABA: top of Mt. Saba, on *Buteo platypterus rivieri* (S.T. Danforth); Hell Gate, on *Oreopeleia mystacea sabae* (S.T. Danforth). — ST. KITTS: (S.T. Danforth). — NEVIS: (James Bond). — MONTSERRAT: on *Butorides virescens maculatus*, *Buteo platypterus rivieri*, *Falco sparverius caribaeorum*, and *Columba squamosa* (S.T. Danforth); on wild dove and sparrow hawk (Hubbard). — GUADELOUPE (recorded by van der Wulp, 1883): Goyave, on *Melanerpes therminieri* (S.T. Danforth). — MARIE GALANTE: Trois Islets, on

Zenaida a. aurita (S.T. Danforth). — DOMINICA: Pointe Michelle (G.A. Ramage). — ST. VINCENT (recorded by Williston, 1896): on *Amazona guildingii* and *Oreopeleia m. montana*; Grand Bonhomme Mts., on *Buteo platypterus antillarum*; Three Rivers Estate, on *Buteogallus anthracinus cancrivorus* (A.R. Totton); windward side (H.H. Smith). — GRENADINES: Beguia I. — GRENADA: St. Andrews, on *Buteo platypterus antillarum* (R. Thaxter).

COLOMBIA (recorded by Falcoz, 1930): without precise locality, on *Buteo m. melanoleucus*; Fusugasugá, Dept. Cundinamarca (Hno. Apolinar-María); Quebrada Susumuco, Dept. Cundinamarca (Hno. Apolinar-María); Villavicencio, Int. del Meta (Hno. Apolinar-María); Valdivia, Dept. Antioquia, on *Chamaepetes g. goudotii* (M.A. Carriker, Jr.); Buenos Aires, Dept. Santander Norte, on *Penelope m. montagnii* and *Columba a. albilinea* (M.A. Carriker, Jr.); Volador, Dept. Bolívar, on *Accipiter b. bicolor*, *Elanoides forficatus yetapa*, *Eurypyga helias major*, *Oreopeleia violacea albiventer*, and *Odontophorus strophium* (M.A. Carriker, Jr.); Vista Nieve, Sa. Marta, Dept. Magdalena, on two *Oreopeleia linearis infusca* (M.A. Carriker, Jr.); Cincinnati, Sa. Marta, Dept. Magdalena, on two *Pionus sordidus saturatus*, one ♀ with 15 Mallophaga attached, and on *Piaya cayana mehleri* (M.A. Carriker, Jr.); Mt. San Lorenzo, Sa. Marta, Dept. Magdalena, on *Penelope argyrotis colombiana* (M.A. Carriker, Jr.); Siminchueva, Sa. Marta, Dept. Magdalena, on *Accipiter erythrocnemius salvini* (M.A. Carriker, Jr.); Mamancanaca, Sa. Marta, Dept. Magdalena, on *Columba a. albilinea* (M.A. Carriker, Jr.); Virolin, Dept. Santander Norte, on *Buteo magnirostris insidiatrix* (M.A. Carriker, Jr.); Guamalito, Dept. Santander Norte, on *Micrastur ruficollis zonothorax* (M.A. Carriker, Jr.); Choachi, Dept. Cundinamarca, on domestic pigeon (Hno. Apolinar-María); Acevedo, Río Suaza, Aguas Claras near San Adolfo, 1400 m., Dept. Huila, on *Chamaepetes g. goudotii* (P. Hershkovitz); 4 kilom. N.E. of Bellavista, near Río Porce, 1200 m., Dept. Antioquia, on *Ortalis columbiana cauceae* (P. Hershkovitz).

VENEZUELA (recorded by Walker, 1849; Bau, 1929): Naignata Peak, Distrito Federal (E.G. Holt); Arabupú, Mt. Roraima, State of Bolívar (A.S. Pinkus); Paulo, at foot of Mt. Roraima, State of Bolívar, on *Buteo m. magnirostris* (T.D. Carter); Rancho Grande, between Maracay and Ocumare-de-la-Costa, State of Aragua, on *Penelope a. argyrotis* and *Urubitornis s. solitaria* (W. Beebe); La Sierra Cojedes, State of Cojedes, 1000 m. (M. Villegas and H. Gines); Caracas (Gellmer); Mérida, on *Accipiter erythrocnemius*

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venezuelensis and on "gavilan" (P. Anduze); Zumbrador, State of Mérida (J.D. Smith); Río Charaito, State of Miranda (G. Vivas-Berthier).

BRAZIL (recorded by Leach, 1817; Lutz, Neiva and da Costa Lima, 1915; Bau, 1929; Falcoz, 1930): without precise locality (Leach's ♀ type of *erythrocephala*); Nova Teutonia near Itá, State Santa Catharina, on *Ictinia plumbea* (F. Plaumann); Rio Grande do Sul (Stiegmayer); São Paulo (J. Lane); Taguara do Mundo Novo, State Rio Grande do Sul, on bird of prey (Strasbourg Mus.); Humboldt, State Santa Catharina, on *Spizaëtus tyrannus* (W. Ehrhardt); Cachoeira, State Rio Grande do Sul, on *Caracara plancus brasiliensis* and *Falco f. femoralis* (W.F. Henninger); Itaquí, State Rio Grande do Sul, on *Falco sparverius eidos* (W. Garbe) and on *Amazona vinacea*; Nova Wurttemberg, State Rio Grande do Sul, on *Spizaëtus ornatus*; São Paulo, State São Paulo, on *Nycticorax nycticorax hoactli*; Sto. Amaro, State São Paulo, on *Buteo m. magnirostris* (Juliani), Porto Cabral, on *Daptrius a. americanus* (J. Lima); Rio Paraná, State Matto Grosso; Guaratuba, State Paraná (A. de St. Hilaire); Paraná (E.D. Jones); Joinville, State Santa Catharina, on *Elanus l. leucurus* (W. Ehrhardt); Theresopolis, State Santa Catharina.

ECUADOR: Baños, Prov. Tungurahua, on small owl (W. Clarke-MacIntyre); Balzapampa (W. Clarke-MacIntyre).

PERU (recorded by Thomson, 1869, as *O. gemina*; Brèthes, 1920; Falcoz, 1930): Tambopata, San Juan, Sandia, Puno, 5000 ft., on domestic fowl (2 ♀) and *Xanthornus decumanus maculosus* (Mrs. H.H. Heller); Yurimaguas, Amazonia, on *Claravis godefrida* ["*Peristera geoffroyi*"]; San Ramon, Valle Chanchamayo, on *Falco deiroleucus* (W. Weyrauch); Pan de Azucar, Río Tarma, 1400 m., on *Oroaëtus isidori* and on wild pigeon (either *Leptotila verreauxi decipiens* or *Columba subvinacea bogotensis*. — W. Weyrauch); Huacapistana, Río Tarma, 1800 m., on *Columba a. albilinea* and *Momotus momota chlorolaemus*, with Mallophaga attached (W. Weyrauch); Lima, on owl (C.H.T. Townsend) and on *Dives dives warszewiczi*, *Tyto alba contempta*, *Zenaida asiatica meloda* and *Zenaidura auriculata hypoleuca* (W. Weyrauch); Valle Chanchamayo (W. Weyrauch and at ParisMus.); Callao (J.J. Walker); Chilpes, 30 miles N.E. of Tarma, on *Pionus tumultuosus* (J. A. Griswold, Jr.); Maraynioc (or Marainioc), 20 miles N.E. of Tarma, on *Cathartes aura jota* (J.A. Griswold, Jr.); Trujillo, on *Asio flammeus suinda* (J. Ortiz de la Puente); Hacienda Cadena, Marcapata, Dept. Cuzco, 1000 m., on *Oroaëtus isidori*, *Mi-*

crastur gilvicollis, *Oreopeleia bourcieri frenata*, and *Pipra chloromeros* (C. Kalinowski); Chanchamayo, Dept. Junín, on "gavilan" (J.M. Schunke).

BOLIVIA: Santa Cruz de la Sierra, 450 m., Prov. del Sara, on *Amazona aestiva xanthopteryx*, with *Mallophaga* attached (J. Steinbach); Incachaca, 2500 m., on *Margarornis s. squamiger* (J. Steinbach); Huachi, Rio Beni (W.M. Mann).

ARGENTINA (recorded by Falcoz, 1930): Campo Grande, Misiones, on *Ramphastos dicolorus* (S. Pierotti); Timbo Viejo, Dept. Burruyacu, Tucumán, on "gavilan" (Carbone); Misiones (E. Kivirikko); Río Salado, Chaco de Santiago (Wagner).

URUGUAY: Laguna Mirim, on *Columba p. picazuro*, July 22 (G. Ivey).

CHILE (recorded by Falcoz, 1930): Valparaiso (d'Orbigny).

O. erythrocephala is restricted to the New World, where it occurs on the continent from Canada to central Chile and Argentina, as well as on most of the West Indian islands.³⁷ The northmost record is from Fort Severn on the Hudson Bay (56° N.), and the southmost from Valparaiso (about 33° S.). In tropical America and the Antilles it is by far the most common bird-fly. Of the 223 localities where it was taken, 16 are in southern Canada, 56 in the United States, 19 in Central America (Mexico to Panama), 69 in the Antilles, and 63 in continental South America. Most North American records are from East of the 100th Meridian, showing the fly's preference for a moist and mild climate.

Known Nearctic Hosts of *O. erythrocephala* (verified individual records in parentheses). Ciconiiformes (1): *Botaurus lentiginosus* (1). Anseriformes (1): *Branta c. canadensis* (1). Falconiformes (56 and 3 undetermined hawks): *Accipiter cooperii* (4); *A. gentilis atricapillus* (1); *A. striatus velox* (7); *Buteo jamaicensis borealis* (3); *B. p. platypterus* (24); *Falco c. columbarius* (8); *F. peregrinus anatum* (2); *F. s. sparverius* (3); *Haliaeetus l. leucocephalus* (2); *Pandion haliaetus carolinensis* (2). Galliformes (2):* *Phasianus colchicus* (2). Columbiformes (1 undetermined pigeon). Strigiformes: *Strix n. nebulosa*. Coraciiformes (1): *Megaceryle alcyon* (1). Piciformes (1): *Sphyrapicus v. varius* (1).

Known Neotropical Hosts of *O. erythrocephala*. Ciconiiform-

³⁷ Bau's record of *O. haitiensis* from New Caledonia (1929b, p. 11) was due either to an erroneous locality label or to a misidentification.

mes (5): *Butorides virescens maculatus* (2); *Leucophoyx t. thula* (1); *Nyctanassa v. violacea* (1); *Nycticorax nycticorax hoactli* (1). Falconiformes (60 and 6 undetermined hawks): *Accipiter b. bicolor* (1); *A. erythrocnemius chionogaster* (1); *A. erythrocnemius salvini* (1); *A. erythrocnemius venezuelensis* (1); *A. gundlachi* (2); *Buteo* sp. (1); *B. j. jamaicensis* (12); *B. jamaicensis costaricensis* (1); *B. jamaicensis umbrinus*; *B. m. magnirostris* (2); *B. magnirostris argutus* (1); *B. magnirostris insidiatrix* (1); *B. m. melano-leucus* (1); *B. platypterus antillarum* (2); *B. platypterus cubanensis* (2); *B. platypterus rivieri* (2); *Buteogallus anthracinus cancrivorus* (1); *Caracara plancus brasiliensis* (1); *Cathartes aura jota* (1); *Circus cyaneus hudsonius* (1); *Coragyps atratus foetens*; *Daptrius a. americanus* (1); *Elanoides forficatus yetapa* (1); *Elanus l. leucurus* (1); *Falco* sp. (1); *Falco c. columbarius* (2); *F. deiroleucus* (1); *F. f. femoralis* (1); *F. peregrinus anatum*; *F. sparverius caribaeorum* (1); *F. sparverius dominicensis* (1); *F. sparverius eidos* (1); *F. sparverius loquaculus* (3); *Herpetotheres c. cachinnans* (1); *Ictinia plumbea* (1); *Leucopternis princeps* (1); *Micrastur gilvicollis* (1); *M. ruficollis zonothorax* (1); *Odon-triorchis palliatus* (1); *Oroaëtus isidori* (2); *Spizaëtus ornatus* (1); *S. tyrannus* (1); *Urubitornis s. solitaria* (1). Galliformes (12): *Chamaepetes g. goudotii* (2); *Dactylortyx thoracicus* (1); **Gallus gallus bankiva* (1); *Odontophorus* sp. (1); *O. guttatus veraguensis* (1); *O. strophium* (1); *Ortalis colombiana cauae* (1); *Penelope a. argyrotis* (1); *P. argyrotis colombiana* (1); *P. m. mon-tagnii* (1); *Penelopina nigra* (1). Gruiformes (1): *Eurypyga helias major* (1). Columbiformes (42 and 3 undetermined pigeons): *Claravis godefrida* (1); *Columba a. albilinea* (3); *C. i. inornata* (2); *C. leucocephala* (4); **C. l. livia* (1); *C. p. picazuro* (1); *C. squamosa* (1); *Columbigallina passerina portoricensis* (1); *Geotrygon versicolor*; *Leptotila j. jamaicensis* (1); *L. v. verreauxi* (1); *Oreopeleia bourcieri frenata* (1); *O. caniceps leucometopius* (1); *O. chrysia* (2); *O. linearis infusca* (1); *O. m. montana* (5); *O. mystacea sabae* (1); *O. violacea albiventer* (1); *Zenaida a. asiatica* (4); *Z. asiatica meloda* (1); *Z. a. aurita* (2); *Z. aurita zenaida* (4); *Zenaidura auriculata hypoleuca* (1); *Z. m. macroura* (2). Psittaciformes (8): *Amazona aestiva xanthopteryx* (1); *A. guildingii* (1); *A. l. leucocephala* (1); *A. ventralis* (1); *A. vinacea* (1); *Aratinga nana*; *Pionus sordidus saturatus* (2); *P. tumultuo-sus* (1). Cuculiformes (2): *Piaya cayana mehleri* (1); *Saurothera v. vetula*; *S. vetula vieilloti* (1). Strigiformes (10 and 2 undeter-mined owls): *Asio flammeus suinda* (1); *A. flammeus portoricensis*

(1); *A. stygius signapa* (1); *Glaucidium siju* (1); *Otus n. nudipes* (1); *Pseudoscops grammicus* (2); *Strix* sp. (1); *Tyto alba contempta* (1); *Tyto alba furcata* (1). Caprimulgiformes (2): *Chordeiles minor gundlachii* (1); *Siphonorhis a. americanus* (1). Trogoniformes (2): *Pharomachrus m. mocino* (1); *Temnotrogon roseigaster* (1). Coraciiformes (1): *Momotus momota chlorolaemus* (1). Piciformes (3): *Melanerpes lherminieri* (1); *M. s. supercilialis* (1); *Ramphastos dicolorus* (1). Passeriformes (9): *Corvus jamaicensis* (2); *Cyanolyca pulchra mitrata* (1); *Dives dives warszewiczi* (1); *Holotrisalis jamaicensis gundlachii* (1); *Margarornis s. squamiger* (1); *Myiobius barbatus atricaudus* (1); *Pipra chloromeros* (1); *Platypsaris niger*; *Xanthornus decumanus maculosus* (1).

Bionomics. *O. erythrocephala* is a typical polyxenous fly. In the Neotropics, where it occurs the year round, it is known from 97 native species (and additional subspecies) of 13 orders: Falconiformes (30), Columbiformes (21), Passeriformes (9), Galliformes (8), Psittaciformes (8), Strigiformes (6), Ciconiiformes (4), Piciiformes (3), Trogoniformes (2), Cuculiformes (2), Caprimulgiformes (2), Coraciiformes (1), and Gruiformes (1). The Falconiformes and Columbiformes head the list and are certainly the chief true breeding hosts, as shown by the verified records: of a total of 164, two-thirds are from these two orders, namely 66, or 39 per cent, from Falconiformes and 44, or 27 per cent, from Columbiformes. The Psittaciformes are probably also breeding hosts, in spite of the few records now available. The captures on the remaining 10 orders are so scattered, that they must be based mainly on strays, except perhaps for the Galliformes and Strigiformes. In the Nearctic Region, where the fly has been taken on 15 native birds of 7 orders, the Falconiformes are even more favored, with 10 host species and 59, or 92 per cent, of the 64 verified records. Of the 10 Raptores listed as hosts from temperate North America, 5 harbor the same fly in the Neotropics. *O. erythrocephala* seems to shun the Columbiformes in the Nearctic Region, as there is only one record, possibly a stray occurrence on a domestic pigeon. The limited host range and relative scarcity north of Mexico, in spite of more intensive collecting, suggest that *O. erythrocephala* may be only an adventitious or seasonal member of the Nearctic fauna. A study of the northern seasonal occurrence further supports this view. The fly has been taken from March 18 on (in New York), through April (Illinois, New York, Nebraska), May (Maine, Michigan, Massachusetts, Montana, Ohio, Maryland,

New York, Minnesota), June (Quebec, Kansas), August (Quebec), September (New York, Illinois), October (New York), and November (New York, to Nov. 16). There is no evidence that it survives as adults in temperate North America on any resident host during the winter or that it hibernates as puparia. It is even doubtful that it breeds to any great extent during the summer in that area. I suspect that it is introduced there afresh every spring on some of its migratory breeding hosts, which might explain why it is so specific of diurnal birds of prey in the United States and Canada, the seasonal migrations of many of these birds being very regular and covering a wide territory.

What little else is known of the life-history of *O. erythrocephala* is reviewed in Part I, pp. 156 (infestation with mites), 172 (phoresy of Mallophaga), and 328 (host relations). The following is an additional case of phoresy: a female on a parrot, *Amazona aestiva xanthopteryx*, at Santa Cruz de la Sierra, Bolivia, carried 4 Mallophaga near dorsal tip of abdomen. A male from Mérida, Venezuela, on "gavilan," has several small mite clusters on the dorsum of the abdomen. Puparium as yet unknown.

Affinities. *O. erythrocephala*, one of the species with relatively short upper orbits, is most nearly related to *O. orizabae*, from which it differs in the shape of the antennal appendage and of the interocular face, as shown in the key. The extensive synonymy results mainly from undue reliance upon variations in the color of the integument and pilosity, which are of little value, as usual in Hippoboscidae. Speiser (1904a, pp. 344-345) recognized that the color of the frons ("labium supra os" of Rondani; "clypeus" of Speiser), used by Rondani to separate *bellardiana* from *erythrocephala*, was unreliable. He retained, nevertheless, *erythrocephala*, *bellardiana* and *haitiensis* as distinct because of other color differences, shown in the subjoined key, while admitting that all three might perhaps be treated rather as varieties.

1. Scutellum dark blackish-brown throughout, at most with a trace of yellowish tinge basally. Bristles of antennal appendage reddish-yellow *O. erythrocephala*
 Scutellum broadly yellowish-brown basally, almost over half the surface 2
2. Bristles of antennal appendage reddish-yellow
 *O. bellardiana*
 Bristles of antennal appendage black or at any rate mixed with black *O. haitiensis*

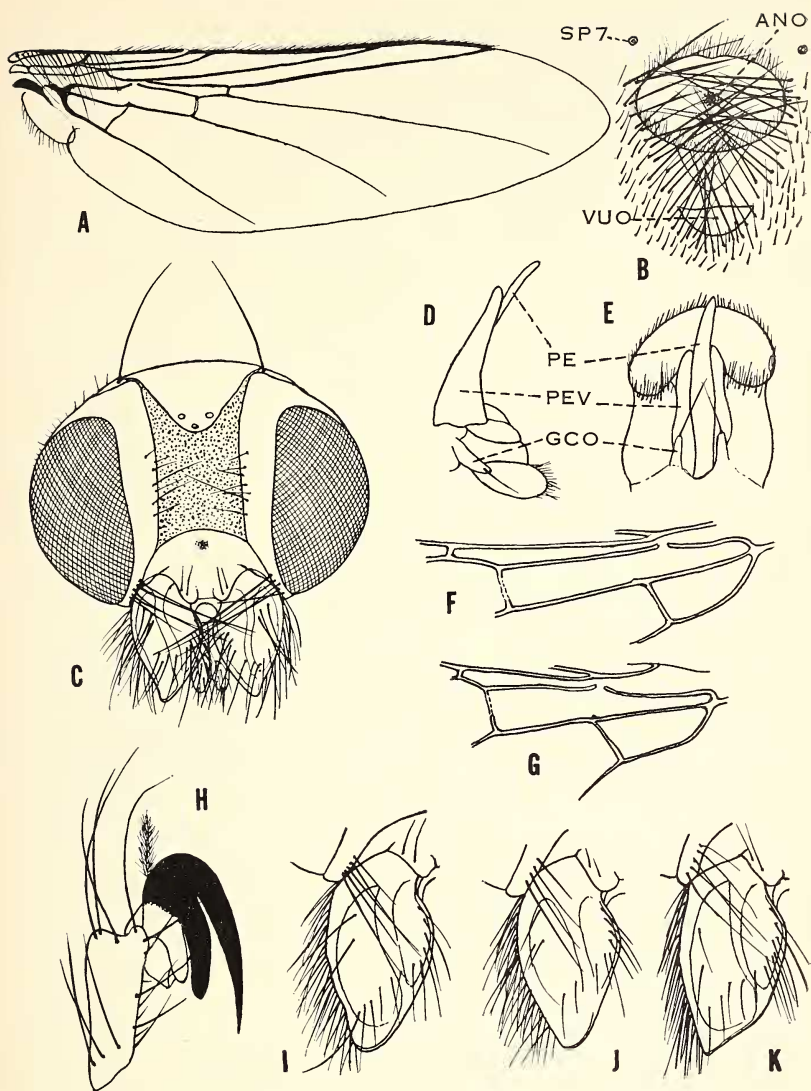


Fig. 38. *Ornithoetona erythrocephala* (Leach). **A**, wing, ♀ type of *O. costaricensis* Swenk, Juan Viñas; **B**, tip of abdomen, ♀, Concord, on *Falco c. columbarius*; **ANO**, anal opening; **SP7**, 7th abdominal spiracle; **VUO**, vulvar opening; **C**, head, ♂, Orient, on *Accipiter striatus velox*; **D-E**, ♂ terminalia in side view (**D**) and from below (**E**), Orient, on *Accipiter striatus velox*: **GCO**, gonocoxite; **PE**, penis; **PEV**, penis valves; **F-G**, basal and anal cells of ♀, St. Vincent, on *Buteogallus anthracinus cancrivorus* (**F**), and Mérida, on "gavilan" (**G**); **H**, distitarsus and claw of hind leg, ♀, St. Vincent; **I-K**, antennae of ♀, Mérida (**I**), St. Kitts (**J**), and Joinville, on *Elanus l. leucurus* (**K**).

Falcoz (1930, pp. 39-40), realizing that Speiser's position was untenable, sunk *haitiensis* and *bellardiana* in the synonymy of *erythrocephala* (his "*hatamensis* Big." on page 40 was an obvious slip for *haitiensis*). My study of many specimens of the large American *Ornithoctona* leads to the same conclusion, as it is impossible to sort them consistently by the color of the scutellum and antennal bristles. Even striking color differences, shown by some flies, cannot be correlated with reliable structural characters or with peculiar geographical or host distributions. Flies taken from one individual bird may differ markedly in color.

The intraspecific variation in the shape of the 3rd antennal segment is more important. Unless it is properly recognized, it might induce misleading attempts to establish distinct species on extreme variants. The average or usual shape is shown in Fig. 38J, in which the inner and outer margins of the appendage converge about equally and gradually over the apical third into a broad, triangular, blunt apex, with somewhat upturned edges. Departures from this are in two directions: in some flies (Fig. 38K) the triangular, blunt apex of the appendage is irregular and shorter, extending only over the apical fifth; in others (Fig. 38I), the apical portion is very broad throughout and the apex is not definitely triangular. Transitions connect all three types, making it impossible to group the specimens consistently on this basis.

The relative length of the anal and 2nd basal cells also varies: the anal may be less than half the length of the 2nd basal, or about half as long, or even slightly more than half (Figs. 38A, F-G). There is no trace of an extra vein in the axillary cell.

As noted by Falcoz (1930, p. 39), the sexual differences of the abdomen are rather conspicuous. In the male, the basal sclerite (combined 1st and 2nd pleurotergites) is short, covered with strong, stiff, curved, almost hook-like setae, longer at the sides; elsewhere the dorsum bears many evenly scattered, short setae; it carries 3 wide but short sclerites, each 4 times as wide as long, fringed with longer setae at the hind margins; a pair of small, setigerous sclerites flank the anal opening; ventrally the integument is membranous and covered with short setae, except for the narrow, trapezoidal, basal sclerite; the genital orifice is surrounded by long setae; terminalia (Figs. 38D-E) as in *Ornithomyia*, but gonocoxites more prominent. In the female, the dorsum of the abdomen lacks median sclerites behind the combined basal pleurotergites; it is uniformly covered medially with short setae, with longer setae at sides and toward apex; there are two small, setig-

erous, lateral, preanal sclerites; female genital opening as in Fig. 38B. The male is smaller than the female, with a wing length of 7.5 to 8 mm. (8 to 10.5 mm. in the female).

Original description of *O. erythrocephala*: "O. corpore perfusco, capite rubro, pedibus fusciscentibus. Caput rubrum infra sordide viridescens-testaceum: labium [frons] albidum. Thorax perfuscus antice sordide testaceus: scutellum perfuscum: pectus sordide viridescens-testaceum: alae pallide fusciscentes: pterigostea [wing veins] marginalia fusca, limbalia alba: pedes fusciscentes infra sordide viridescens-testacei: tarsi quatuor anteriores sordide testacei nigro-marginati, postici nigri: ungues atri. Abdomen luteum nigricans-hirsutum: dorsum saturatius." There is a brief diagnosis on p. 7: "Corpore perfusco, capite rubro, pedibus fusciscentibus." I have seen the ♀ type in 1951 at the British Museum. Speiser (1902) and Austen (1903) recognized that it is the common large American species of *Ornithoctona*. The parts originally described as dull-greenish have now turned dirty-yellow, without a trace of green. According to Dr. G.B. Fairchild (*in litt.*, 1953), the wing is 9.6 mm. long.

Original description of *O. nebulosa*: "Head yellow; feet pale; tibia with two reddish-brown lines. Eyes blackish-brown; vagina and hypostoma, pale; thorax reddish-brown, with a large yellowish humeral spot and three longitudinal lines, of which the intermediate one includes an impressed line, which interrupts a transverse impressed line; humeral angle prominent, subacute; spiracle white; marginal nervures blackish-brown, those of the disk brown; scutell reddish-brown, varied with yellow at base; pectus [sternum] yellow-white, anterior margin bifurcated; tarsi dark reddish-brown, nails black; abdomen pale-brownish, with black hair, first segment on its anterior face pale-yellow. Length $\frac{3}{8}$ inch [7.5 mm.]. The type is lost; but the description and size agree exactly with *O. erythrocephala*, and there is no other large hippoboscid in the United States that could possibly fit it. The statement about the bifurcated anterior margin of the sternum should particularly be noted. It is remarkable that *erythrocephala* has not been taken again on the type host of *nebulosa*, although there are records from other species of owls in the West Indies and South America.

Original description of *O. gemina*: "Lata, testacea, thorace apice emarginato, postice piceo, abdomine supra fusco; fronte ocellis distinctis, utrinque linea subarcuata impressa; alis flavescentibus, nervo transverso-ordinario pone postcoastae exitum sito. ♀ Long. 8 mill. Caput parvum, margine postice arcuato thoraci bene adaptatum; fronte [interocular face] linea utrinque integra, subincurva impressa; epistomate [frons] brevi, postice arcu impresso a fronte [interocular face] discreto; antennis magnis, lamellatis, horizontaliter deplanatis, ovalibus, glabriculis, margine externo acuto densius et interno parcius fulvo-setosis; palpis brevibus, vix corneis, sub antennis occultis; oculis maximis lateralibus, testaceis, pupilla interiore nigra ovali rotunda. Thorax apice semicirculariter emarginatus, callo humerali nigro-setoso, spinoso-producto; scutello transverso, margine postico late rotundato. Alae nervis corneis, costali cum ramo submarginali in 6:a parte posteriore conjuncto ibique desinente, abscissa 2:a 3:a sextuplo longiore, hac quam nervo transverso vix longiore, 4:a 5:a saltem duplo longiore; post-costali medium alae haud attingente; transverso-ordinario pone postcoastae exitum, ante medium alae sito: cellula humerali longa, nervo transverso subobliquo, pallido, mox ante postcoastae exitum sito, oclusa; anali nervo transverso bene oclusa. Abdomen latum, suturis inter segmenta vix conspicuis. Pectus [sternum] testaceum, inter coxas anticas utrinque spinoso-productum. Pedes intermediis posticis longiores, testacei, parvi pilosi; tibiis linea superna et inferiore nigro-picea notatis; tarsis posticis articulo 1:o 5:o brevioribus, hoc unguiculis 3-dentatis, pulvillis magnis et empodio distincto praedito." The type, which I saw at the Stockholm Museum in 1933, is a ♀ of *O. erythrocephala*, as Speiser (1904) recognized.

Original description of *O. bellardiana*: "Long. mill. 7-8. Corpus nigropiceum; capite, margine anteriore thoracis aut saltem humeris, scutelli vitta basali magis vel minus manifesta, vel rubescente-testaceis vel rufis. Oris labium [frons], et antennae capite concoloria; istis latis et longis, organa oralia tegentibus, et fulvo-pilosis. Abdomen dorso nigricante, basi plus minusve anguste pallida, apice luride albicante, ventre obscure fuscio. Alae paulo et aequaliter fusciscentes etiam angulo interiori: vena secunda longitudinale costam attingente contra, nisi fere ante transversam anteriorem: distantia tertiae in costale a secunda, magis quam dupla distantiae a quarta: vena transversa intermedia longior aut sub-aequale distantia ab exteriori. Pedes sordide glauci, femoribus superioribus fuscis: tibiis antice et postice anguste nigricante-marginatis: tarsis obscuris, posteriorum articulis basalibus intus sub-glaucois." Rondani placed his species among those with last section of costa somewhat shorter than penultimate section. He stated that it differed from *O. batchiana* and *O. haitiensis* [both synonyms of *Ornithoetona plicata* v. Olfers] in the "pilis antennarum fulvescentibus non nigris"; and from *O. erythrocephala* in the "labro supra os [frons] non albido, sed capite rufescente concolore; abdomine non luteo sed nigricante." He described more than one specimen, at least one being kept in his collection, its present location being unknown. Another was probably returned to the Genoa Museum, where I have seen a ♀ of *O. erythrocephala* now labelled "*pyrrhocephala* Rondani." I agree with Speiser (1904), who also saw this fly, that this was no doubt an earlier manuscript name given by Rondani to what he later called "*bellardiana*," so that I regard it as one of the cotypes. Speiser found the color of the frons unreliable; but he thought that *bellardiana* and *erythrocephala* could be separated by the color of the scutellum and of the setae of the antennal appendages, though admitting that these also might be variable, so that possibly the two forms should be regarded as varieties of one species. A large series of *erythrocephala* shows that all these color variations, not only intergrade, but are influenced by extraneous factors, such as age.

Original description of *O. haitiensis* (French text translated): "Long 7 mm. Antennis et capite fulvis, nitidis, nigro setosis. Thorace nitido, flavidofulvo, macula fusca transversa, lata, subcordiformi, notato; scutello nitido, fusco, utrinque, basi, pallide fulvo; abdomine castaneo, opaco, basi obscure fulvido; pedibus fulvis, tarsis apice, posticis, omnino, fuscis, femoribus posticis et intermediis linea exili laterali, tibiis superne et inferne, angustissime fuscis; alis pallide flavidis, venis, costali, longitudinalibus 1-4is, omnino, 5a et 6a, usque ad venas transversas, nigris, transversali 1a nigra, 2a pallida. Head and antennae fulvous, with black setae; epistoma [frons] with a rounded pit; vertex [postvertex] and sides of frons [inner orbits] shiny; ocelligerous spot blackish; thorax and scutellum shiny; the former pale fulvous with a large, nearly heart-shaped, brown dorsal spot; the latter brown with two yellowish basal spots at sides and with fairly numerous black, stiff setae near hind margin; abdomen dull, brownish with somewhat yellowish base; legs fulvous-yellow, with rather long black bristles; tips of tarsi (hind tarsi entirely) blackish; a thin, longitudinal brown line on outer face of mid and hind femora; all tibiae margined with brown above and below; wings pale yellowish; costa and 1st to 4th longitudinal veins entirely, 5th and 6th longitudinals as far as cross-veins, blackish; 1st or outer [anterior] cross-vein blackish, the 2nd [anterior basal] white; 1st and 4th longitudinals (of Rondani's terminology) ending in costa not far from each other, a little beyond inner [anterior basal] cross-vein; 3rd reaching costa close to 4th; two basal cells fairly unequal." Speiser (1902) examined the type, now in Mr. J.E. Collin's collection, where I also saw it (1951). He recognized that it was closely related to *erythrocephala*, but thought that it differed in a reliable color character of the scutellum. He stated also: "According to the original description, *erythrocephala* has the scutellum 'perfuscum,' which color is also present in many specimens seen by me. On the other hand, in *O. haitiensis* the scutellum is broadly yellow at the base, as

Rondani described it also for his *O. bellardiana*. Bigot's species differs from *bellardiana* clearly in the black, not reddish-yellow setae of the antennal appendages. The clypeus [frons] of *haitiensis* is not as bright reddish-yellow as in most other specimens referable to the same species group, yet is not strictly white. I do not believe, moreover, that Leach's specimen had actually a white clypeus (which Leach calls the labium); for, if Leach's species is actually as widely distributed and occurs on as great a variety of birds as Walker mentions, I should have found at least one with a white clypeus among the many specimens of the group now before me. Concerning the shape of this clypeus [frons] in *O. haitiensis*, it should also be noted that, while it looks angularly emarginate in the middle of the anterior margin when seen from above, it is found, upon more careful examination, that the slightly convex clypeus [frons] is sunken between the antennal appendages and bears here, exactly in the middle, a deep pit, which, moreover, is set off by its dark brown color from the pale yellowish-brown surrounding area. The small pit at the hind margin, also present in *O. erythrocephala*, was previously noted by Bigot. Concerning the venation, it may be mentioned briefly that the subcosta ends in the costa mid-way between the anterior and the posterior cross-veins, the last section of the costa is over half the length of the penultimate, the second basal cell is shorter than the first for about the length of the posterior cross-vein and twice as wide as the first, and the anal cell is about exactly half as long as the 2nd basal cell. Legs without peculiarities; color of tarsi as described for *O. erythrocephala*." I have discussed before Speiser's later (1904) attempt to distinguish 3 species in what I can only regard as the one *O. erythrocephala*.

Original description of *O. robusta*: "♂ ♀. Brown; front, antennae and legs rufous; wings brownish-hyaline; first vein ending in the costa above the small cross-vein; 4th portion of the costa much longer than 5th. Length 7 mm. The ocelli are less conspicuous than in *O. avicularia* and only recognizable in the 3 impressed points on the posterior frontal plate. Front [interocular face] rufous and, except the median space, very glossy, in the ♂ as broad as the eyes, in the ♀ much broader; antennae coniform, rufous, and hairy. Thorax reddish-brown; the humeral prominences [callosities] dentiform. Abdomen dark brown. Legs rufous; femora thick and, as well as the tibiae, with long bristly hairs; the foot-claws black, strong. Wings brownish; 1st vein reaching the costa above the small cross-vein, which stands distinctly before the middle of the wing; the auxiliary vein reaches the costa near the end of the 1st vein, the 2nd vein close to the termination of the 3rd (the 3rd portion of the costa, that is, between the auxiliary and the 1st veins, thus being very small and the 4th portion very large and much longer than the 5th); the 2nd basal cell is a little shorter than the superior [first], and the cross-vein by which it is closed is often inconspicuous; the inferior basal cell (anal cell) is trigonal and rather indistinct. In its large size, general facies, neuration of the wings, etc., this species much resembles *O. columbae* Wiedem. from Java, Borneo, etc., but is probably distinct, the habitat being very different." Austen (1903) recognized that all 5 cotypes were ♀ (not 1 ♀ and 4 ♂, as v. d. Wulp stated), and that they could not be separated from *O. erythrocephala*, a conclusion with which I agree after seeing the specimens in 1951. According to Dr. G.B. Fairchild (*in litt.*, 1953), the length of the wings is as follows: ♀ with type label, from Caché, 10 mm.; ♀ from Volcán de Chiriquí, 10.2 mm.; ♀ from Zapote, 9.5 mm.; ♀ from Jalapa, 9.6 mm.

Original description of *O. buteonis*: "Length 7-7.5 mm. Head yellowish-brown, the broadly crescentic orbital margins and the vertex [postvertex] polished, the median area opaque. Clypeus [frons] convex, slightly emarginate and rather weakly pitted anteriorly and bearing a small round pit on the posterior margin. Antennary processes distinctly less than twice as long as broad, clothed with bright pale ferruginous hair, broadly lanceolate owing to both margins being evenly convex, the tips narrowly rounded. Eyes light brown. Thorax

above fuscous-brown, paling to testaceous on the humeral angles, the inner margins of the dentiform processes and the adjacent spiracle whitish. Mesoscutum with a feeble median impressed line and deep, sinuate, lateral median transverse impressed lines. Scutellum fuscous brown, strongly tinged with reddish on the anterior margin, discally shallowly depressed, and bearing a row of about a half dozen short black hairs near each margin. Under side of head and thorax pale testaceous, the labium whitish at tip. Legs above reddish-brown, below pale testaceous, the tibiae with the edges fuscous, the tarsi fuscous, the claws black. Abdomen yellowish, copiously but not densely clothed with short, black hairs. Wings clear, the costal veins and bases of the longitudinal veins dark brown, the 1st longitudinal vein ending in the costa at a point nearly above the 1st cross-vein, the costal border of the marginal cell about one fourth longer than the costal border of the 1st submarginal cell and the 1st cell more than the length of the 2nd cross-vein longer than the 2nd basal cell. Belongs to the *O. erythrocephala* group. Agrees with *O. erythrocephala* Leach, of Brazil to Mexico and the West Indies, in size and venation, but differs in the reddish-brown rather than ferruginous head, the concolorous clypeus [frons], the darker legs and the reddish anterior border of the scutellum. *O. nebulosa* Say, from the western United States, is the same size, but differs in the clypeus [frons] being pale (concolorous with the rest of the head in *buteonis*), and the reddish-brown mesonotum with three yellowish lines (fuscous-brown without markings in *buteonis*). From *O. fusciventris* Wiedemann, described from Kentucky, *buteonis* differs in larger size (*fusciventris* is only 5 mm. long), somewhat less deeply emarginate anterior border of clypeus [frons] (deeply and angularly emarginate in *fusciventris*), flattish scutellum (basally inflated in *fusciventris*) and in the coloration of the thorax being much darker than the head (concolorous in *fusciventris*). *O. pilosula* van der Wulp, from Costa Rica, is smaller (5.5 mm.) and has the head and thorax rufous. *O. haitiensis* Rondani, from Haiti, is distinct in its dark-haired antennae and different venation, the 1st longitudinal vein ending in the costa before the 1st cross-vein. This latter venational character will also separate *O. avicularia* Linnaeus, the common European species, and *O. varipes* Walker, of Mexico to Colombia and Peru, the latter further differing in the shape of the antennary process. *O. anchineuria* Speiser (= *O. pallida* Say) may be distinguished at once by the interstitial 1st and 2nd cross-veins, making the 2nd basal cell nearly as long as the 1st basal cell (much shorter in *buteonis*). The coloration is entirely different from *O. butalis* Coquillett, described from Bering Island." I was able to study the holotype and paratypes of *buteonis* at the University of Nebraska in 1940 and again in 1953. Both are ♀ and agree in every structural detail with *O. erythrocephala*. The supposed differences pointed out by the author have in my opinion no specific value in the genus *Ornithoctona*. The wing of the holotype is 10.4 mm. long.

Original description of *O. costaricensis*: "Length 7 mm. Front [clypeus] and vertex wholly glossy bright ferruginous, the posteriorly broadening orbital margins and the vertex triangle [postvertex] perfectly smooth and polished, the median area microscopically tessellated, giving it a satiny luster, and of subuniform width. Clypeus [frons] concolorous with front [mediovertex] and vertex [postvertex], anteriorly medially emarginate because of a deep rectangular pit, posteriorly also with a large, deep, oval pit. Antennary processes twice as long as broad, their sides convex and their tips narrowly rounded, of a darker ferruginous color than the clypeus and front and provided with long, ferruginous hairs. Eyes glossy black. Humeral prominences pale, heavily black-haired. Mesonotum shining blackish, slightly suffused with reddish along the anterior sutures, bearing a faintly impressed median line and deep, slightly curved, transverso-median depressions on each side of it. Scutellum rounded posteriorly, medially much depressed transversely and this depression bearing several long, black hairs, shining black like the mesonotum but with the anterior margin red-

dish testaceous, interrupted medially by a blackish stain. Sternum and under side of head greenish testaceous. Legs beneath greenish testaceous, above fusco-testaceous, becoming dusky on the tibiae, fuscous on the tarsi and with the claws black. Abdominal tegument dark brown, but so heavily clothed with black hairs as to appear blackish. Wings slightly clouded, the costal veins and bases of the longitudinal veins blackish, the 1st longitudinal vein ending in the costa slightly before the 1st cross-vein, the costal border of the marginal cell fully twice as long as the costal border of the 1st submarginal cell, and the 1st basal cell twice the length of the 2nd cross-vein longer than the 2nd basal cell. The shiny blackish mesonotum seems to distinguish this species from all of the described North American congeners except *O. butalis* Coquillett, which is much smaller (4 mm.), has the front black spotted on the orbits and vertex with yellow, and is otherwise very different. The species is really close to *O. erythrocephala*, but apparently differs in the deep anterior pit on the clypeus, the red anterior border on the scutellum, and, compared with van der Wulp's description of *O. robusta* which Austen places as a synonym of *erythrocephala* after a comparison of the types of both in the British Museum, it should also differ in darker legs and abdomen, although these color differences are not clear from a comparison with Leach's original description of *erythrocephala*. From *O. haitiensis* it differs at once in the ferruginous hairs on the antennary process, the dark legs and the different venation (the 1st longitudinal vein ends considerably before the 1st cross-vein and the costal border of the marginal cell is less than twice as long as the costal border of the 1st submarginal cell in *haitiensis*). The venational characters are much like those of *O. buteonis*, just described, and separate the species from several of its congeners." I examined the type of *costaricensis* at the University of Nebraska in 1940 and again in 1953 and found that it is a female of *O. erythrocephala*. The differentiating characters, mostly of color, mentioned in the description are not of specific value in this genus. The wing of the type is 10.5 mm. long.

Original description of *O. albiventris* (translated from the German): "Of the group of *O. erythrocephala*. Abdomen grayish-white, densely and finely punctate with black, entirely bare above and below, hairy only at base, somewhat at side margins and more strongly at apex. Head bright red, anteriorly somewhat more pale yellowish. Vertex [interocular face] medially with a broad, flat depression [mediovortex], above the antennae with smaller depressions. Eyes brown. Ocelli brown. Antennal appendages with reddish-yellow setae. In the specimen seen, neck clearly visible and grayish-white. Notum dark bluish-gray, darker, almost black medially, paler on sides, with a well-marked, bright red, longitudinal streak and a strong transverse depression. Humeral protuberances more yellowish-gray, with black setae. Scutellum bluish-gray, scarcely paler basally, with fine markings of sculpture and with black setae posteriorly. Coxae and sternum yellowish flesh-color; upper femora of the same color, bearing only few, long black setae (as compared with related species). Fore tibiae without spur. Tibiae above bluish-gray, beneath yellowish flesh-color or dirty yellow, with many black setae. Tarsi blackish-gray, the segments somewhat yellowish in the middle above. Claws black. Wings pale brownish-gray. Venation not differing specially from *O. erythrocephala*. First two longitudinal veins (subcostales) end close together in costa shortly before and somewhat above small [anterior] cross-vein. Third section of costa very short, 4th section somewhat longer than 5th. Anterior [1st] basal cell narrow; posterior [2nd] broad, its width about $\frac{3}{4}$ of length of posterior cross-vein. Anal cell scarcely half the length of posterior [2nd] basal cell. Abdomen grayish-white, without any yellowish tinge, closely covered with fine small punctations, dorsally and ventrally entirely bare, black setose only at base (somewhat more strongly) and at sides (sparsely); with strong, black bristles around the black anus. Penultimate abdominal segment, at a distance from middle line of about $\frac{1}{4}$ of width of abdomen, with two large, black spots seemingly formed by densely

crowded, minute, swollen punctations. As stated before, anus black, with black setae. Total length of specimen in alcohol, 10.8 mm.; from mouth to hind margin of scutellum, 5.5 mm.; of wing, 10.5 mm." Bau says it differs from related species "in the abdomen being completely bare above and below and in the sparsely setose upper femora. . . . The abdomen is grayish-white, punctate with black. In the other species the abdomen is yellowish-gray, brownish or blackish, always without black punctations." The description fits specimens of *erythrocephala* perfectly, and, although I have not seen the type, which should be at the Berlin Museum, I do not hesitate to synonymize *albiventris*. The black punctations of the abdomen were, I believe, the insertions of the usual short setae.

Ornithoctona orizabae, new species

Figs. 39A, 43G-H, and 44B

Male. Head (Fig. 43G) seen in front about $1\frac{1}{3}$ times as wide across eyes as high from occipital margin to bottom of frontal emargination. Interocular face at its narrowest about half the width of an eye, nearly twice as high as wide; inner eye margins slightly converging toward lower third. Inner orbit much less than half the width of mediovertex at its narrowest; orbital bristles few and weak: 3 or 4 (one very long) at side of lunula; a short row of 3 at about mid-height; 1 rather short vertical bristle. Upper orbit rapidly narrowed laterally, shorter than width of inner orbit at ptilinal suture. Postvertex broadly triangular, slightly wider than long, smooth, evenly rounded anteriorly; ocelli well developed, placed far down and close together; anterior ocellus much, and posterior ocelli slightly, below a line drawn through upper eye margins. Frons: lunula with a shallow basal depression, separated by a slight suture from the lower, very narrow and short interantennal portion, which is broadly emarginate at apex; apical arms short and weak, hidden beneath inner edges of antennal appendages. Antenna (Fig. 43H): 1st segment with 1 or 2 short setae, almost fused with lunula, except for a short, but deep groove at interantennal area of frons and a faint trace of a suture elsewhere. Appendage of 2nd segment about as long as half the height of head (from occipital margin to bottom of frontal emargination), longer in proportion to width than in most other *Ornithoctona* (except *O. nitens*), about 3 times as long as greatest width; basal $\frac{2}{3}$ nearly parallel-sided, apical $\frac{1}{3}$ gradually narrowed, triangular, with blunt apex; surface only superficially grooved, setulose as usual. Palpi short and thick, not extending beyond antennal appendages. Head beneath with many long bristles (vibrissae) in several irregular rows on side ridges of rostrum membrane. Thorax (Fig. 44B) as usual in *Ornithoctona*, but relatively narrower,

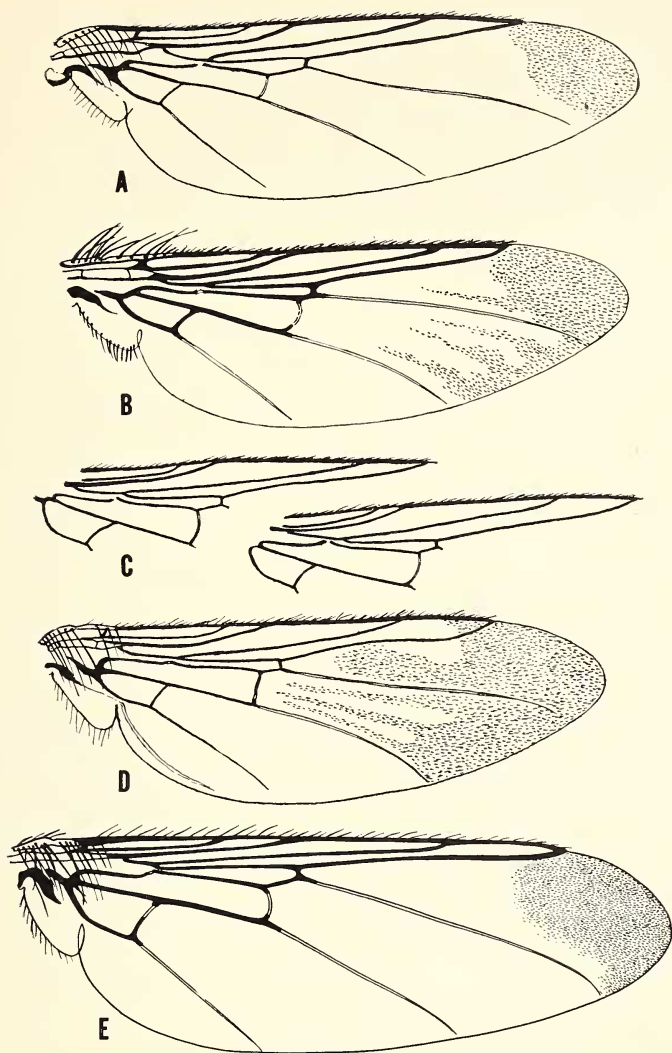


Fig. 39. Wings of *Ornithoetona*: **A**, *O. orizabae* J. Bequaert, ♂ holotype, Orizaba; **B-C**, *O. fusciventris* (Wiedemann), ♀, Nebraska (**B**), ♀, Usaquen (**C**, left), and ♀, Wellesley (**C**, right); **D**, *O. oxycera* Falcoz, ♀, El Jonquito; **E**, *O. (Ornithopertha) nitens* (Bigot), ♀, Turrialba, on *Trogon* sp.

longer and slightly more convex dorsally than in *O. erythrocephala*; scutellum relatively longer and more produced behind; ventrally, prosternal lobes somewhat curved. Chaetotaxy of thorax as in *O. erythrocephala*, except for a single notopleural bristle; other setae shorter and thinner than in that species. Legs unusually slender; femora much thinner than in *O. erythrocephala*, with weaker and sparser setae; tips of tibiae normal; hind basitarsus beneath with the usual transverse, basal comb of short setae. Wing (Fig. 39A) with typical *Ornithoetona* venation; but anterior and anterior basal cross-veins farther apart than usual (distance between them on 4th longitudinal more than length of anterior basal); relative length of anal and 2nd basal cells nevertheless about as in *O. erythrocephala*; no trace of extra vein in axillary cell; membrane with a patch of microtrichia in apical third of 1st posterior cell, not quite reaching 4th longitudinal and extending only slightly basad of tips of costa and 3rd longitudinal. Abdomen not suitable for an adequate description in its present shrivelled condition; the usual dorsal median sclerites of the male sex appear to be present, the preanal pair very large. Male terminalia, protruding distinctly from apex of abdomen, differing, so far as visible, little from those of *O. erythrocephala*. The dried, pinned type is colored like many *O. erythrocephala*: head mostly reddish-brown; thorax dark mahogany-brown with dirty-yellow humeral areas, scutellum and legs; wings slightly smoky throughout, with blackish-brown veins; setae of body, including those of antennae, black.

Length, from tips of antennal appendages to hind margin of scutellum, 5 mm.; of wing, 10 mm.; width of wing, 3 mm.; total length of dry, shrivelled specimen, 6.5 mm.

MEXICO: Orizaba, State of Vera Cruz, from unknown host (A. Sallé), ♂ holotype (British Museum, Natural History).

Affinities. *O. orizabae* is closely related to the common *O. erythrocephala*. I have ventured to describe it from one specimen, because the narrow frons, combined with the peculiar shape of the 2nd antennal segment, seems to differentiate it clearly. Although the 2nd antennal segment varies in *erythrocephala*, that of *orizabae* is well outside the range of these variations.

Ornithoetona fusciventris (Wiedemann)

Figs. 39B-C, 40, 41, 42, 43A-F, and 44C

Ornithomyia fusciventris Wiedemann, 1830, Aussereurop. Zweifl. Ins., 2, p. 611 (no sex; no host. Kentucky. Type ♀ in Vienna Mus.). Osten Sacken, 1858, Cat. Dipt. North America, p. 86; 1878, Smithson. Misc. Coll., No.

- 270, p. 213. Rondani, 1878, Ann. Mus. Civ. Stor. Nat. Genova, 12, p. 158 (Mexico: on *Piranga flava hepatica*). Aldrich, 1905, Smithsonian Misc. Coll., 46, No. 1444, p. 654.
- Ornithoctona fusciventris* Speiser, 1905, Zeitschr. Syst. Hym. Dipt., 5, p. 348 (synonymy of *O. chilensis* Guérin); 1907, Ent. News, 18, p. 103; 1908, Zeitschr. Wiss. Insektenbiol., 4, pp. 303 and 304. J. Bequaert, 1940, Mem. Soc. Cubana Hist. Nat., 14, No. 4, pp. 315 and 317. Stuardo, 1946, Catálogo Dípteros Chile, p. 187. MacArthur, 1948, Bull. Publ. Mus. Milwaukee, 8, pt. 4, p. 403, figs. 238-239 (Michigan: East Lansing, on *Hedymeles ludovicianus*. Illinois: Beach, on *Accipiter striatus velox*. Minnesota: on *Hedymeles ludovicianus*. Wisconsin: Milwaukee Co., on *Wilsonia canadensis*). Thompson, 1949, Ent. Mo. Mag., 85, p. 248 (Jamaica: Newcastle Road, St. Andrew, on *Seiurus a. aurocapillus*; Hermitage, St. Andrew, on *Mniotilta varia*). J. Bequaert, 1950, Agricultura Técnica, Santiago de Chile, 10, pt. 1, p. 8.
- Ornithomyia chilensis* Guérin-Ménéville, 1835, Iconographie Règne Animal, Insectes, Atlas, Pl. 104, fig. 5 (with name; dated as drawn November, 1835; no locality or description. Type probably lost). Macquart, 1843, Mém. Soc. R. Agric. Arts Lille, (for 1842), p. 437 (no sex; no host. Chile. Described as a new species, but based on the same specimen as Guérin's species, which Guérin sent to Macquart) [1843, Dipt. Exot., 2, pt. 3, p. 280]. Not of E.P. Reed, 1904.
- Ornithomyia chiliensis* Guérin-Ménéville, 1844, Iconographie Règne Animal, Insectes, Text, p. 556 (no sex; no host. Chile. Type from "Voyage de la Coquille," probably lost). Girard, 1885, Traité Élémentaire d'Entomologie, 3, p. 1068; Atlas, Pl. 116, fig. 5 (copy of Guérin's fig. of 1835, uncolored).
- Ornithoctona chilensis* J. Bequaert, 1933, Rev. Chilena Hist. Nat., 37, p. 163.
- Ornithomyia testacea* Macquart, 1845, Mém. Soc. R. Sci. Agric. Arts Lille (for 1844), p. 346 (no sex; no host. Colombia. Type originally in Fairmaire Coll., later in Bigot Coll., now in J. E. Collin Coll.) [1846, Dipt. Exot., Suppl. 1, p. 218]. J. Bequaert, 1940, Rev. Acad. Colombiana Cienc. Ex. Fis. Nat., 3, No. 12, p. 417.
- Ornithoctona testacea* Speiser, 1902, Zeitschr. Syst. Hym. Dipt., 2, p. 180 (re-description of type in J. E. Collin Coll.).
- Ornithomyia varipes* Walker, 1849, List Dipt. Brit. Mus., 4, p. 1146 (no sex; no host. Colombia. Type ♀ at Brit.Mus.). Speiser, 1904, Ann. Mus. Civ. Stor. Nat. Genova, 41, p. 348 (regards it as distinct from *O. obsecurata* Walker); 1907, Ent. News, 18, p. 103; 1908, Zeitschr. Wiss. Insektenbiol., 4, p. 304. J. Bequaert, 1940, Rev. Acad. Colombiana Cienc. Ex. Fis. Nat., 3, No. 12, p. 417.
- Ornitheza* (?) *varipes* Austen, 1903, Ann. Mag. Nat. Hist., (7), 12, p. 262 (in part: Walker's type, van der Wulp's specimen of "*O. avicularia*" from Río Sucio, Costa Rica, and the specimens from Huamachuca, Peru, 3000 m., and Orizaba, Mexico). Aldrich, 1905, Smithsonian Misc. Coll., 46, No. 1444, p. 653.
- Ornithomyia pilosula* van der Wulp, 1903, Biol. Centr.-Amer., Diptera, 2, p. 432; Pl. 13, figs. 6-6a (? ♀; no host. Costa Rica: Volcán de Irazú. Type ♀ at Brit.Mus.). Austen, 1903, Ann. Mag. Nat. Hist., (7), 12, p. 262 (type; says it is probably an *Ornitheza*). Speiser, 1907, Ent. News, 18, p. 103 (says it is not an *Ornitheza*); 1908, Zeitschr. Wiss. Insektenbiol., 4, p. 304.
- Ornitheza pilosula* Aldrich, 1905, Smithsonian Misc. Coll., 46, No. 1444, p. 653. Bau, 1929, Zoolog. Anzeiger, 85, p. 11 (Brazil: Conganhas).
- Ornithoctona parva* Speiser, 1902, Zeitschr. Syst. Hym. Dipt., 2, p. 180 (no sex; no host. Colombia. Description of a specimen called *O. parva* by

- Macquart in Bigot's Coll., now in the J. E. Collin Coll., but not Macquart's type). Not *Ornithomyia parva* Macquart, 1843.
- Ornithomyia parva* J. Bequaert, 1940, Rev. Acad. Colombiana Cienc. Ex. Fis. Nat., 3, No. 12, p. 417 (Speiser's specimen from Colombia).
- Ornithomyia avicularia* van der Wulp, 1903, Biol. Centr.-Amer., Diptera, 2, p. 431 (Costa Rica: Río Sucio). Not of Linnaeus, 1758.
- Ornithomyia pirangae* Swenk, 1916, Jl. New York Ent. Soc., 24, p. 135 (no sex. Costa Rica: Juan Viñas, on *Piranga r. rubra*. Type ♀ in Dept. Entom., Univ. Nebraska, Lincoln). Muma, 1952, Bull. Univ. Nebraska State Mus., 3, pt. 3, p. 14 (type).
- Ornithomyia strigilecula* Ferris, 1923, Parasitology, 15, p. 57, figs. 3 and 14A-C (♀, larva; no host. Peru: Lima. Type in California Ac. Sci., San Francisco, mounted on 2 slides, No. 1473). Hennig, 1952, Larvenformen der Dipteren, 3, p. 402.
- Ornithoetona strigilecula* Ferris, 1924, Ent. News, 35, p. 234. Falcioz, 1930, Encyclop. Entom., Diptera, 5, (for 1929), p. 40 (Peru: Río Mixiolla, 1200 m., Prov. Huallaga. Colombia: on *Poecilothraupis igniventris lunulata* and *Conirostrum rufum*. Argentina: Villa Lutezia near San Ignacio, Misiones). Peters, 1936, Bird-Banding, 7, p. 25 (Maryland: on *Hedymeles ludovicianus*). J. Bequaert, 1940, Rev. Acad. Colombiana Cienc. Ex. Fis. Nat., 3, No. 12, p. 415. Procter, 1946, Biol. Surv. Mt. Desert, 7, Insect Fauna, p. 437 (no specimen). Schuurmans Stekhoven, 1952, Beiträge zur Fauna Perus, 3, Wissenschaftl. Bearbeit., pp. 94 and 101.
- "Louse-fly" Lugger, 1897, 2nd Ann. Rept. State Entom. Minnesota, (for 1896), p. 144, fig. 124 (Minnesota: on *Hedymeles ludovicianus*). Washburn, 1905, Univ. Minnesota, Agric. Expt. Sta., Bull. 93, p. 163, fig. 161.

Distribution and Specimens Examined. DOMINION OF CANADA. ONTARIO: Narrows of Lake Abitibi, on *Wilsonia canadensis* (N.K. Bigelow); Lockton, on *Piranga erythromelas* (C. Hope); Ghost River, Lake Abitibi, June 27, on *Vireo philadelphicus* (N.K. Bigelow). — QUEBEC: Chelsea, on *Hedymeles ludovicianus*, May 27 (J. Fletcher).

UNITED STATES. CALIFORNIA: Marin Co.—CONNECTICUT: without precise locality, on *Hedymeles ludovicianus* (S.W. Williston). — DISTRICT OF COLUMBIA: Mt. Hamilton, on *Empidonax virescens* (P. Bartsch). — ILLINOIS (recorded by MacArthur, 1948): Beach, Lake Co., on *Accipiter striatus velox* (W.W. Dearborn). — KENTUCKY (recorded by Wiedemann, 1830): Wiedemann's ♀ holotype, without more precise locality. — MARYLAND (recorded by H.S. Peters, 1936): Laurel, Prince Georges Co., on *Hedymeles ludovicianus*, May 14 (E.B. Marshall). — MASSACHUSETTS: Wellesley, Norfolk Co., May 20, 1902 (M.C.Z., from C.W. Johnson Coll.). — MICHIGAN (recorded by MacArthur, 1948): East Lansing, Ingham Co., on *Hedymeles ludovicianus* (W.B. Barrows). — MINNESOTA (recorded by Lugger, 1897; MacArthur, 1948): without precise locality, on *Hedymeles ludovicianus*, June 23 (O. Lugger; specimen recorded by him in 1897, without name). — NEBRASKA: without

precise locality (M.C.Z., from Loew Coll.). — NEW JERSEY: Mantua, Gloucester Co., on *Setophaga r. ruticilla*, July 4 (Carl L. Pedersen). — NEW YORK: without precise locality (J. Akhurst, in Osten Sacken Coll. at M.C.Z.); Ithaca, Tompkins Co., on *Dendroica tigrina*, May 18 (W. Montagna). — PENNSYLVANIA: Reading, Berks Co., (L.S. Dillon). — VIRGINIA: Falls Church, Fairfax Co., on *Dendroica tigrina* (N. Banks). — WASHINGTON (STATE): Pullman, Whitman Co., Oct. (L.R. Campbell). — WISCONSIN (recorded by MacArthur, 1948): Milwaukee Co., on *Wilsonia canadensis*, May 20 (O.J. Gromme). — Also one specimen from the United States, without precise locality, on *Piranga erythromelas*.

MEXICO (recorded by Rondani, 1878; Austen, 1903, as *O. varipes*): 8 kilom. E. of San Cristobal Las Casas, State of Chiapas, on *Junco phaeonotus fulvescens* (R.A. Paynter, Jr.); off the coast of Yucatan, on board ship, Apr. 25, 1952 (A.E. Holmes); Santa Rosa, Comitán, State of Chiapas, on *Piranga l. leucoptera* and *Momotus momota lessonii* (Esc.N.C.Biol.); Orizaba, State of Vera Cruz (A. Sallé).

GUATEMALA: Finca Samac, Alta Vera Paz (L.C. Stuart).

COSTA RICA (recorded by van der Wulp, 1903, as *O. pilosula* and *O. avicularia*; Swenk, 1916, as *O. pirangae*): Juan Viñas, on *Piranga r. rubra* (type of *pirangae* Swenk. — L. Bruner); Río Sucio; Volcán de Irazú (type of *O. pilosula*).

PANAMA: Boquete, Chiriqui Prov., on *Pseliophorus tibialis*, with 2 Mallophaga attached; Barriles, W. of El Volcán, Chiriqui Prov., on *Cercomacra tyrannina rufiventris*, *Euetheia olivacea pusilla*, *Lipaugus h. holerythrus*, *Odontriorchis palliatus*, *Empidonax flavescens*, and *Henicorhina leucophrys collina* (Mrs. M.E. McClellan Davidson); Salta, Boquete, Chiriqui Prov., on *Turdus plebeius*, *T. tristis cnephosa*, and *Piranga bidentata sanguinolenta* (G.F. Ferris); Cerro Azul, Boquete, Chiriqui Prov., on *Atlappetes gutturalis*.

ANTILLES. JAMAICA (recorded by Thompson, 1949): Newcastle Road, St. Andrew, 2000 ft., on *Seiurus a. auropillus* (G.B. Thompson); Hermitage, St. Andrew, 1800 ft., on *Mniotilta varia* (G.B. Thompson). — HISPANIOLA: Morne Tranchant, Haiti (J. Bend); Massif de la Selle, Haiti (A. Wetmore); Constanza, Rep. Dominicana, on *Dendroica pinus chrysoleuca* and *Zonotrichia capensis antillarum* (W.L. Abbott).

COLOMBIA (recorded by Macquart, 1845, as *O. testacea*; Walker, 1849, as *O. varipes*; Speiser, 1902, as *O. parva*; Falcoz, 1930, as *O. strigilecula*): without precise locality (type of *O. varipes*); Meta

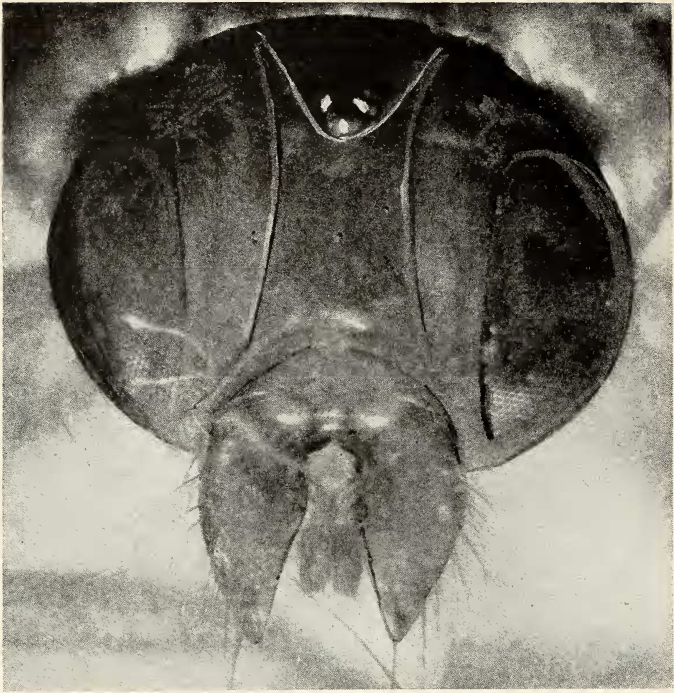


Fig. 40. *Ornithoetona fusciventris* (Wiedemann), head, ♀ holotype, Kentucky. Photograph by Mr. K. MacArthur (1948, fig. 239).

District (B. Guevara); Angostura, Dept. Santander Sur, on *Xanthoura yncas cyanodorsalis* (M.A. Carriker, Jr.); Piedecuesta, Dept. Santander Sur, on *Atlapetes schistaceus tamae*, *Cinnycerthia u. unirufa*, *Grallaria r. rufula*, *Dubusia t. taeniata*, *Zonotrichia capensis costaricensis*, *Synallaxis u. unirufa*, and *Turdus fuscater gigas* (M.A. Carriker, Jr.); Volador, Dept. Bolivar, on *Tachyphonus x. xanthopygius* (M.A. Carriker, Jr.); Palo Gordo, Dept. Santander Norte, on *Lepidocolaptes affinis lachrymiger*, *Tachyphonus rufus*, and *Platycichla flavipes leucops* (M.A. Carriker, Jr.); Buenos Aires, Dept. Santander Norte, on *Scytalopus sylvestris* (M.A. Carriker, Jr.); Vista Nieve, Sa. Marta, Dept. Magdalena, on *Chamaepetes goudotii sanctae-marthae* and *Scytalopus femoralis sanctae-martae* (M.A. Carriker, Jr.); Cincinnati, Sa. Marta, Dept. Magdalena, on *Momotus momota subrufescens* (M.A. Carriker, Jr.); Pamplona, Dept. Santander Norte, on *Poecilothraupis igniventris lunulata* (M.A. Carriker, Jr.); Virolin, Dept. Santander Norte, on

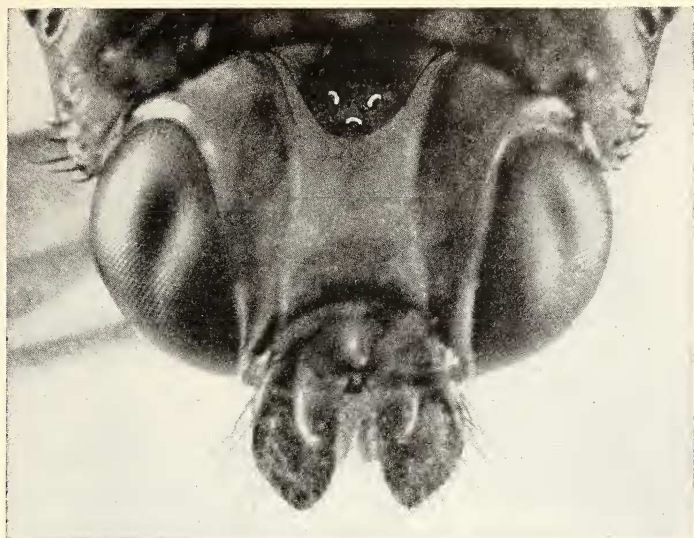


Fig. 41. *Ornithoetona fusciventris* (Wiedemann), head, ♀, Milwaukee Co., on *Wilsonia canadensis*. Photograph by Mr. K. MacArthur (1948, fig. 238).

Calospiza arthus aurulenta (M.A. Carriker, Jr.); Fusugasugá, Dept. Cundinamarca, on *Conirostrum rufum* and *Sturnella magna meridionalis* (Hno. Apolinar-María); Choachi, Dept. Cundinamarca, on *Poecilothraupis igniventris lunulata* (Hno. Apolinar-María); Usaquen, Dept. Cundinamarca (E. Osorno M.); Aguadita, on *Conirostrum rufum* (Hno. Apolinar-María).

VENEZUELA: Summit of Mt. Duida, Territory of Amazonas (Tyler Duida Exp.); Mt. Roraima, State of Bolívar (T.D. Carter); Camp Benitez, N. slope of Mt. Marahuaca, 4000–5000 ft., Territory of Amazonas (J. Maldonado C.).

BRAZIL (recorded by Bau, 1905, as *O. pilosula*): Rio de Janeiro (E.G. Holt); Vermelho, 30 Kilom. N. of Cara Pintada, on Rio das Marrecas, State of Paraná, on *Sclerurus s. scansor* and *Thamnophilus caerulescens gilvigaster* (Polish Zool. Exp.); near Cachoeira, State of Rio Grande do Sul (W.F. Henninger); São Paulo, State of São Paulo, on *Thamnophilus c. caerulescens*; Maromba, Itatiaia, State of São Paulo (J. Lima); Mogi dos Cruzes, State of São Paulo, on *Thamnophilus c. caerulescens*; Boraceia, State of São Paulo, on *Thamnophilus c. caerulescens*; Fazenda Boa Esperanza, S. José da Lagoa, State of Minas Gerais, on *Colonia c. colonus*.

ENTOMOLOGICA AMERICANA

ECUADOR: Baños-Mera trail, 1200 m., Dept. Tungurahua (J. Clarke-MacIntyre).

PERU (recorded by Austen, 1903, as *O. varipes*; Ferris, 1923, and Falcoz, 1930, as *O. strigilecula*): Chanchamayo, 1500–2000 m. (Strasbourg Mus.); Oreja de Capelo near Pan de Azucar, Río Tarma, on *Accipiter erythrocnemius ventralis* (W. Weyrauch); Pan de Azucar, Río Tarma, on *Zonotrichia capensis peruviansis* (W. Weyrauch); Maraynioc (or Marainioc), 20 miles N.E. of Tarma, on *Poecilothraupis l. lachrymosa* (J.A. Griswold, Jr.); Río Mixiollo, 1200 m., Prov. Huallaga (G.A. Baer); Hacienda Cadena, Marcapata, Cuzco, 1000 m., on *Thamnophilus melanchrous* and *Thlypopsis sordida chrysopis* (C. Kalinowski); Lima (R.H. Beck. — Holotype ♀ of *O. strigilecula*).

ARGENTINA (recorded by Falcoz, 1930, as *O. strigilecula*): Tafi del Valle, 2300 m., Province Tucumán, on *Muscisaxicola fluviatilis* (R. Golbach); Villa Lutecia near San Ignacio, Misiones (Wagner).

CHILE (recorded by Guérin-Méneville, 1844, as *O. chilensis*).

O. fusciventris is restricted to the New World, where its distribution parallels that of *O. erythrocephala*. The fewer records may be due in part to the small size and the preference for Passeriformes, on which flies are more difficult to collect than on pigeons and birds of prey. Nevertheless it appears to be more tropical, not extending as far north and south in the temperate areas, where it is perhaps a sporadic, casual summer visitor. The northmost records are from Chelsea, Quebec (45° 30' N.), in the East and Pullman, Washington (46° 40' N.), in the West; the southmost from northern Argentina (between 27° and 28° S.). Many gaps remain to be filled in the distribution. Of the 75 localities where *O. fusciventris* was taken, 4 are in southern Canada, 18 in the United States, 12 in Central America (Mexico to Panama), 5 in the Antilles, and 36 in continental South America. In the United States the records are scattered over the entire territory.

Known Nearctic Hosts of *O. fusciventris* (verified individual records in parentheses). Falconiformes (1): *Accipiter striatus velox* (1). Passeriformes (14): *Dendroica tigrina* (2); *Empidonax virescens* (1); *Hedymeles ludovicianus* (5); *Piranga erythromelas* (2); *Setophaga r. ruticilla* (1); *Vireo philadelphicus* (1); *Wilsonia canadensis* (2).

Known Neotropical Hosts of *O. fusciventris*. Falconiformes (1): *Accipiter erythrocnemius ventralis* (1). Galliformes (1): *Chamaepetes goudotii sanctae-marthae* (1). Coraciiformes (2): *Momotus momota lessonii* (1); *M. momota subrufescens* (1). Pas-

seriformes (49): *Atlapetes gutturalis* (1); *A. schistaceus tamae* (1); *Calospiza arthus aurulenta* (1); *Cercomacra tyrannina rufiventris* (1); *Cinnycerthia u. unirufa* (1); *Colonia c. colonus* (1); *Conirostrum rufum* (2); *Dendroica pinus chrysoleuca* (1); *Dubusia t. taeniata* (1); *Empidonax flavescens* (1); *Euetheia olivacea pusilla* (1); *Grallaria r. rufula* (1); *Henicorhina leucophrys collina* (1); *Junco phaeonotus fulvescens* (1); *Lepidocolaptes affinis lachrymiger* (1); *Lipaugus h. holerythrus* (1); *Mniotilta varia* (1); *Muscisaxicola fluviatilis* (1); *Odontriorchis palliatus* (1); *Piranga bidentata sanguinolenta* (1); *P. flava hepatica*; *P. l. leucoptera* (1); *P. r. rubra* (1); *Platycichla flavipes leucops* (1); *Poecilothraupis igniventris lunulata* (2); *P. l. lachrymosa* (1); *Pselliophorus tibialis* (1); *Sclerurus s. scansor* (1); *Scytalopus femoralis sanctae-martae* (1); *S. sylvestris* (1); *Seiurus a. aurocapillus* (1); *Sturnella magna meridionalis* (1); *Synallaxis u. unirufa* (1); *Tachyphonus rufus* (1); *T. x. xanthopygius* (1); *Thamnophilus c. caerulescens* (3); *T. caerulescens gilvigaster* (1); *T. melanchrous* (1); *Turdus fuscater gigas* (1); *T. plebeius* (1); *T. tristis cnephosa* (1); *Thlypopsis sordida chrysopsis* (1); *Xanthoura yncas cyanodorsalis* (1); *Zonotrichia capensis antillarum* (1); *Z. capensis costaricensis* (1); *Z. capensis peruviansis* (1).

Bionomics. *O. fusciventris* will no doubt be recognized as one of the important bird-flies of the American tropics and subtropics. Although the 8 Nearctic and 46 Neotropical birds listed above can be only a fraction of the actual hosts, evidently the fly's true breeding hosts are Passeriformes (7 of the 8 Nearctic species, with 14 of 16 verified records; 43 of the 46 Neotropical species, with 49 of 53 verified records). The records are too fragmentary for detailed analysis, as few birds are represented by more than one capture; the fly may have a predilection for the Thraupidae (12 records from 11 species), a large, strictly American family of birds. *O. fusciventris* seems to replace *Ornithomyia fringillina* and *Ornithomyia parva* on Passeriformes in tropical America, perhaps owing to climatic factors rather than to interspecific competition. In temperate North America *O. fringillina* is known from 4 of the 8 species on which *fusciventris* was found. Moreover, the scarcity of North American records, in an area so well collected for hippoboscids, suggests that *fusciventris* is not truly indigenous there the year round. Most probably it is unable to survive through the winter in most of the Nearctic Region, either as adult flies on winter residents or as puparia; if so, it must be introduced afresh each spring on migratory birds returning from farther south.

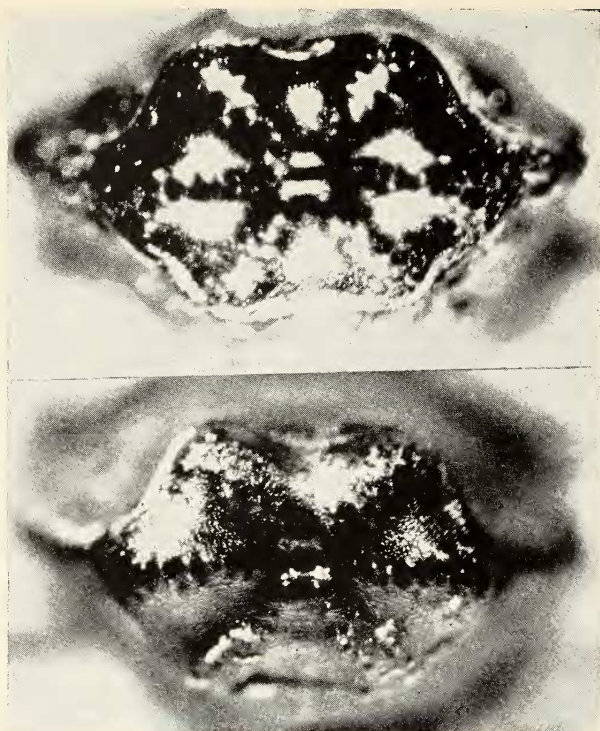


Fig. 42. *Ornithoetona fusciventris* (Wiedemann), 2 views of cap with respiratory lobes of puparium, Tafi del Valle. Photographs by Dr. W. L. Nutting.

Ferris described a larva of *O. fusciventris* deposited by a fly from Lima, Peru (1923, p. 58, fig. 4B, as *O. strigilecula*). I received from Dr. A. Willink a puparium deposited by a fly taken on *Muscisaxicola fluviatilis* at Tafi del Valle. This is entirely black, broadly elliptical in contour, somewhat depressed, equally convex dorsally and ventrally, 3.2 mm. long, 3 mm. wide, and 2.2 mm. thick. Two light longitudinal depressions, one dorsal and one ventral, run along each side margin, a short distance from the edge; the larval segmentation is superficially shown by 8 broad, shallow, transverse grooves, slightly interrupted medially and stopping at the lateral longitudinal depressions. A shallow notch encloses the small "buccal papilla" or cephalic segment anteriorly. Posteriorly, a large hexagonal cap, with rounded angles (Figs. 42), comprises the two polypneustic, spiracular lobes separated by a small but deep median pit; each lobe is divided by wide, shallow radiating depres-

sions in 3 broad, convex ridges, each bearing 12 to 15 irregularly placed pores on minute raised tubercles. The integument, devoid of setae or spines, is moderately shiny and microscopically alutaceous owing to a minute network of fine, close set engraved lines.

Additional information on the bionomics was included in Part I, pp. 156 (infestation with mites), 172 (phoresy of Mallophaga), and 321-322 (host relations).

Affinities. Among the species of *Ornithoctona* with long upper orbits, *O. fusciventris* is most closely related to the Indo-Pacific *O. australasiae* (Fabricius, 1805) (see J. Bequaert, 1941*b*, p. 269, for synonymy, from which *O. soror* Ferris, 1926, should be deleted, however) and the African *O. laticornis* (Macquart, 1835) (= *O. platycera* Macquart, 1843). These 3 species are about the same size and agree in the extent of the microtrichia in the wing. *O. australasiae* differs from the others in the relatively higher head, which is only about $1\frac{1}{4}$ times as wide as the height (from occipital margin to notch of frons) and in the antennal appendage being narrower throughout, with convex outer margin and nearly straight inner margin. In both *O. fusciventris* and *O. laticornis*, the head is about $1\frac{1}{3}$ times as wide as the height and the inner margin of the antennal appendage is distinctly convex; the only consistent difference between them appears to be that in *laticornis* the appendage ends in a longer and sharper point (about as in *oxycera*, but without the laterally compressed tip) than in *fusciventris*.

In *O. fusciventris* the venation is so variable (Figs. 39*B-C*) that few specimens have it exactly alike. The last section of the costa varies from about $\frac{1}{3}$ to slightly less than $\frac{2}{3}$ of the penultimate section. The position of the tip of the 1st longitudinal in relation to the anterior and anterior basal cross-veins, the distance between these two cross-veins on the 4th longitudinal, as well as the relative length of the 2nd basal and anal cells are also most unreliable; in some flies the anal cell is almost half the length of the 2nd basal, but in most it is decidedly less. The axillary cell shows sometimes a weak trace of an extra vein in the shape of a broad, linear convexity.

The 2nd antennal segment or appendage varies within even wider limits in *O. fusciventris* than in *O. erythrocephala*, as may be seen from the two extremes in the photographs of Figs. 40 and 41. One could easily be tempted to regard these two types as marking distinct species, if a series of flies did not show all gradations between them (Figs. 43*C-F*). It is, moreover, impossible to find other

reliable differences correlated with the two antennal types, although the more pointed antenna is more common.

As in most *Ornithoctona*, the lunula of *O. fusciventris* bears a more or less pronounced median depression or pit; anterior to this, the short, deep remnant of the suture dividing the 1st antennal segment from the lunula lies in a slight depression on either side of the narrow interantennal area; the depressions are sometimes deep enough to simulate a pair of pits. These pits are not a specific character.

Original description of *O. fusciventris* (German text translated): "Mellea; abdomine fusco, pedibus viridibus. Honey-yellow, with brown abdomen and green legs. Length $2\frac{1}{2}$ lines [Danish lines = 5.1 mm.]. Head and dorsum of thorax uniformly honey-yellow, with a reddish-yellow tinge, somewhat brownish on hind part of thorax; head anteriorly with a brown semi-lunar spot. Clypeus [frons] with a short angular emargination. Under side of head and thorax very pale yellow, the lip [gula] even white. Impressed cross-shaped line of notum distinct. Scutellum as in the European *O. avicularia*: flat apically, convexly raised basally. Abdomen brown, with 3 smooth transverse points [sclerites], basally with the usual transverse swelling or fold. Wings yellowish: veins brownish-black, their course exactly as in *avicularia*. Legs green; only outermost margins of femora and tibiae, as well as surface of hind femora, somewhat brownish." The ♀ type passed from Wiedemann to Winthem and later to the Vienna Natural History Museum. It was loaned to Mr. K. MacArthur, who sent it to me for study and who made the photograph of the head (Fig. 40). It agrees with the smaller of the two common American species of *Ornithoctona*. Wing 6 mm. long; total length of dry specimen about 5 mm., of combined head and thorax 3.2 mm.

Original description of *O. chilensis* Guérin (translated from the French): "Head and thorax fulvous-yellow, smooth, shiny. Abdomen ochre-yellow, very hirsute. Wings transparent; veins black near costa, yellow elsewhere. Legs testaceous; upper margin of fore and mid femora and all tibiae brown. Tarsi yellowish; tips of segments brown; claws black. Length $5\frac{1}{2}$ mm." As Speiser (1905) recognized, the size and figure refer it to *O. fusciventris*, even though this species has not been collected again in Chile. The following description by Macquart (1843) was based on the same specimen, now presumably lost, as he states that it was collected during the voyage of "La Coquille" and given to him by Guérin: "Picca. Pedibus flavis. Long. 2 l. [2 French lines = 4.5 mm.]. Pitch-brown. Legs yellowish." This description appeared before the text of Guérin's work, but after the Plate of the Atlas, which carries the specific name.

I have explained before why I use the name *Ornithomyia parva* Macquart (1843) for the common species of *Ornithomyia* of temperate South America, called *O. remota* by Walker (1849). I also mentioned the specimen from Colombia, labelled "*O. parva*" by Macquart and now in the Bigot Collection (in Mr. J.E. Collin's possession). Speiser (1902) recognized that this is an *Ornithoctona* and described it as follows (translated from the German): "Length as in the preceding species [*O. testacea* Macquart, the type of which is 4.5 mm. long]. Ground color umber-brown, with paler, more yellowish-brown humeral callosities and a more reddish-brown head. Frons [interocular face] relatively much wider, occupying half or more of width of head, narrowed anteriorly. Vertical triangle [postvertex] wider than long. Clypeus oris [frons] with only a median pit, which is, however, decidedly deeper than the 3 pits of the preceding species. Scutellum of the usual shape, with a median furrow showing

cross-wrinkles and widened posteriorly. Terminal section of costa only half as long as penultimate. Remainder as in preceding species [*O. testacea*].” My study of this specimen in 1951 has shown that it is a ♀ conspecific with *Ornithoctona fusciventris* (Wiedemann). The anterior ocellus is just on the level of the upper margins of the eyes and the wing is 6.5 mm. long.

Original description of *O. testacea* (French text translated): “Testacea. Abdomine griseo. Long. 2 l. [2 French lines=4.5 mm.]. Head (including eyes) and thorax shiny testaceous. Abdomen grayish. Legs green; tarsi black. Wings somewhat yellowish.” Speiser (1902) recognized it as an *Ornithoctona* and redescribed the type as follows (translated from the German): “Length 4.5 mm.; from oral margin to hind margin of scutellum, 3 mm. Head, thorax and legs almost uniformly testaceous; at most margins of antennal appendages darker and humeral callosities somewhat paler. Sculpture of clypeus oris [frons] very striking: it bears 3 small pits, one in the middle behind, and before this a symmetrical pair. Frons [interocular face] narrow, occupying only $\frac{1}{3}$ of width of head, exactly parallel-sided. Vertex [occipital margin] evenly rounded; vertical triangle [postvertex] wider than long. Thorax with fairly long and pointed humeral callosities, with a broadly interrupted transverse suture, otherwise without special features. Legs without special characters; fore tibiae without spur. Wings without peculiarities. Apical section of costa a little over half the length of penultimate; subcosta ending before small [anterior] cross-vein. Posterior [2nd] basal cell shorter than anterior [1st] basal cell for less than the length of the posterior [anterior basal] cross-vein; anal cell not quite half the length of posterior [2nd] basal cell.” I also studied this type in 1951, reaching the conclusion that it is not separable from *O. fusciventris*, a common fly in Colombia. Antennal appendages about twice as long as wide (length to width, 50 : 23); anterior ocellus exactly on the level of upper margins of eyes; wing 6 mm. long, with a few microtrichia near tip; interocular face wider than eye (ratio, 27 : 19). The sex could not be determined in the present condition of the specimen.

Original description of *O. varipes*: “Fulva, verticis vitta antice picea, thorace bisulcato, abdomine piceo, pedibus fulvis, femoribus basi viridibus, tibiatarum vittis tarsisque piceis, alis limpidis. Body dark tawny, smooth, shining; front of the head and mouth beset with bristles; crown with a broad dull stripe, whose fore border is pitchy; eyes pitchy; two indistinct furrows on the chest, one longitudinal, the other transverse quite obsolete at the point of intersection: abdomen pitchy, dull, clothed with black hairs; legs tawny, beset with black bristles; thighs at the base bright green; shanks with pitchy streaks; feet pitchy; claws black, long; wings colourless; wing-ribs pitchy; fore border veins black, the other veins dull tawny. Length of body 2 lines [4.3 mm.]; of the wings [span of wings] 5 lines [10.6 mm.].” Austen (1903) examined the type and thought that it might be an *Ornithoeza*, a genus unknown at present in the New World. He also could not separate it from *Ornithomyia obscurata* Walker (1861), described from Celebes, and he referred to *varipes* the following specimens at the British Museum: van der Wulp’s (1903) supposed *Ornithomyia avicularia*, from Rio Sueio, Costa Rica, a ♀ from Huamachuca, Peru, a ♀ from Orizaba, Mexico, and a ♀ from Molokai, Hawaii. In 1951 I examined the type and the other specimens at the British Museum. The type I regard as a ♀ of *Ornithoctona fusciventris*: antennae large and leaf-like; venation as in *Ornithoctona* (not as in *Ornithoeza*); interocular face twice as wide as an eye; anterior ocellus placed near the level of upper margins of eyes; the one remaining, incomplete wing measures 4.9 mm. to the tip of the 3rd longitudinal, giving 6.3 to 6.5 mm. for the complete wing. van der Wulp’s specimen from Costa Rica, and the flies from Peru and Mexico are (as Austen stated) conspecific with *O. varipes*, hence also *Ornithoctona fusciventris*. The specimen from Molokai is an *Ornithoctona* and most probably also the American *O. fusciventris* (not *Ornithoeza metallica* as I suggested in 1941b, p. 260); the palpi are unfor-

tunately destroyed, making the specific determination difficult. As for the type of *O. obscurata*, it is a ♀ of the Indo-Malayan and Pacific *Ornithoctona australasiae* (Fabricius), which is, moreover, closely related to *O. fusciventris*, as mentioned above.

Original description of *O. pilosula*: "♀ ? Head and thorax rufous; abdomen dark brown; legs yellowish, hairy; wings brownish-hyaline; first vein ending in the costa above the small cross-vein; 4th and 5th portions of the costa nearly of the same length. Length 5.5 mm. Agrees in most respects with the European *O. avicularia*: the front [interocular face] is broader than the eyes; the semilunar plate before the antennae [lunula] has a rather deep impression; the ocelli are distinct; the end of the auxiliary vein is close to that of the 1st vein; and the inferior basal (anal) cell is present and complete. It differs, however, in having longer and more numerous hairs on the femora and tibiae, the somewhat more elongate form, and also in the neuriation: the 1st vein ends in the costa just above the small cross-vein, the latter being more retracted towards the base of the wing; the 4th portion of costa (between the 1st and 2nd veins) is as long as the 5th (between the 2nd and 3rd veins)." Austen published (1903) the following notes on the type: "This species closely resembles *O. varipes* Walker, in size and general appearance. The antennary processes, however, although large and lanceolate, are narrower than in that species, more elongate and more pointed at the tips. Their apical halves are somewhat divergent, and the species should probably be assigned to the genus *Ornitheza*. It is stated by van der Wulp that *O. pilosula* agrees in most respects with the European *O. avicularia*; but the shape of the antennary processes is entirely different. The figure of the head (v. d. Wulp's Pl. 13, fig. 6) is misleading, since it gives no idea of the orbital margins, which, like those of *O. varipes*, are greatly expanded posteriorly." Dr. F. van Emden wrote me (1951) that the type is a ♀, with a wing length of 6.78 mm. (5.37 mm. to tip of 3rd vein); antennae leaf-shaped, though somewhat narrower than in the type of *varipes*; ocelli well-developed, placed above a line drawn through upper margins of eyes; width of interocular face as in *varipes*; 2nd longitudinal vein free throughout from costa; section of costa between tips of 2nd and 3rd veins practically as long as preceding section, while in *varipes* it is only half as long. My personal study of the type in 1951 confirmed these observations. I consider *O. pilosula* as conspecific with the common *Ornithoctona fusciventris*. As shown before, the outline and relative width of the antennal appendage, as well as the relative length of the sections of the costa and other details of the venation, vary within specific limits in this, as in other species of *Ornithoctona*.

Original description of *O. pirangae*: "Length 4.5 mm. Head and thorax above shining brownish testaceous, clearing to yellowish testaceous on the lower orbital margins, vertex [postvertex], anterior margin and median line of mesonotum and base of scutellum. Orbital margins, broadening posteriorly and vertex [postvertex], polished, the median area [mediovertex] conspicuously duller and of subuniform width throughout. Clypeus [frons] anteriorly medially emarginate and bearing a small, shallowly rounded pit, most of its dorsal surface involved in a large, oval, deep pit. Antennary processes a little less than twice as long as broad, the outer margins strongly convex and the inner margins nearly straight, causing the pointed tips to appear divergent, in color fusco-testaceous and clothed with dark hairs. Eyes brown. Mesonotum with a slight median longitudinal depression and somewhat stronger transverse, slightly sinuate, median lateral depressions. Scutellum slightly convex and with a slight transverse depressed line near apex which bears 4 strong black bristles. Under side of head and thorax shining pale testaceous, the long spines on anterior coxae and the labium whitish. Legs greenish testaceous, paler beneath, the tarsi infuscated and the claws black. Abdomen yellowish, copiously but not densely clothed with short, black hairs. Wings clear, the costal veins and bases of the longitudinal veins black, the 1st longitudinal vein ending in the costa

above the 2nd [anterior basal] crossvein and considerably before the 1st [anterior] crossvein, the costal border of the marginal cell a little less than twice as long as the costal border of the 1st submarginal cell and the 1st basal cell as much longer than the 2nd basal cell as the length of the 2nd [anterior basal] crossvein. This species is apparently closest to *O. haitiensis* Bigot, with which it agrees in the dark hair on the antennary processes and the 1st longitudinal vein ending in the costa before the 1st [anterior] crossvein, but differs in its smaller size (*haitiensis* is 7 mm. long), in the form of the clypeus [frons] (*haitiensis* has a small dorsal pit, but a large and deep angular anterior pit) and in the coloration (*haitiensis* has a large, well-defined, cordiform mesonotal area, a black ocellar spot, etc.). It differs at once from *O. erythrocephala* Leach and *O. bellardiana* Rondani in the dark instead of ferruginous hairs on the antennal processes. Its small size separates it at once from the described North American forms except *O. butalis* (which has a very different coloration), *O. anchineuria* (which has the basal cells of subequal length) and *O. fusciventris* (which has the head and mesonotum uniformly colored).'' The type, examined at Lincoln in 1940 and again in 1953, is a ♀ agreeing in every respect with what is here called *Ornithoctona fusciventris*. The wing is 6 mm. long. It should be noted that the color of the setae on the antennal appendages, head and thorax is of no specific value in this genus.

Original description of *O. strigilecula*: "Female. General color dark brown. Length 6 mm. Head distinctly broader than long; dorsal side destitute of setae except for a pair at the anterior margin of the orbits and a small orbital pair farther back; ventral side with a row of small setae paralleling the orbits and a cluster on a prominence at each side of the palpi; antennae noticeably large, about half as long as the head, flat, tapering to a point anteriorly and bordered by many slender setae; palpi slightly shorter than the antennae, bearing numerous small setae. Thorax with the humeral angles strongly produced and bearing several long black setae and several small, stout setae just before the wing; mesonotum destitute of setae except for one long one at the base of the wing and two widely separated long ones behind the wing; scutellum with a few very small marginal setae and a median cluster of 3 quite long setae. Ventral side with no setae except for a row in front of the middle coxae; mesosternum produced anteriorly into a pair of processes which surpass the anterior coxae. Legs with no especially distinctive characters except for the presence on the first segment of the hind tarsi of a distinct comb of small, stout setae. Wings of the type common to the genus, the setulae arranged in a definite pattern as shown, the posterior margin not ciliate. Abdomen with the basal tergite very short, beset medially with many small setae, these giving way laterally to long setae; the dorsum bearing 3 small, median, chitinated areas and thickly beset with small slender setae except for the apical area; apical area with a pair of small chitinated areas which bear 3 long setae. Basal sternite small, with a marginal series of small, stout setae; remainder of the venter thickly beset with setae of which those of the median region are small and slender and those of the marginal areas and about the vaginal opening are long and slender. Spiracles quite small." The author added that its most distinctive features, as compared with *O. lagopodis* (= *fringillina*) and *O. avicularia*, are the presence of the ventral comb on the hind basitarsi and the anterior prolongations of the mesosternum. He referred it later (1924) to *Ornithoctona*. From the description and figures it is easily recognized as *O. fusciventris*, and I confirmed this identity by studying the type slides at San Francisco in 1953.

Ornithoctona oxycera Falcoz

Figs. 39D, 43I-K, and 44 E

Ornithoctona oxycera Falcoz, 1930, Eneyclop. Entom., B, Diptera, 5, (for 1929), p. 36, figs 1-3 (♀. Colombia: Bogotá, on *Buteo* [*Geranoaëtus*] m.

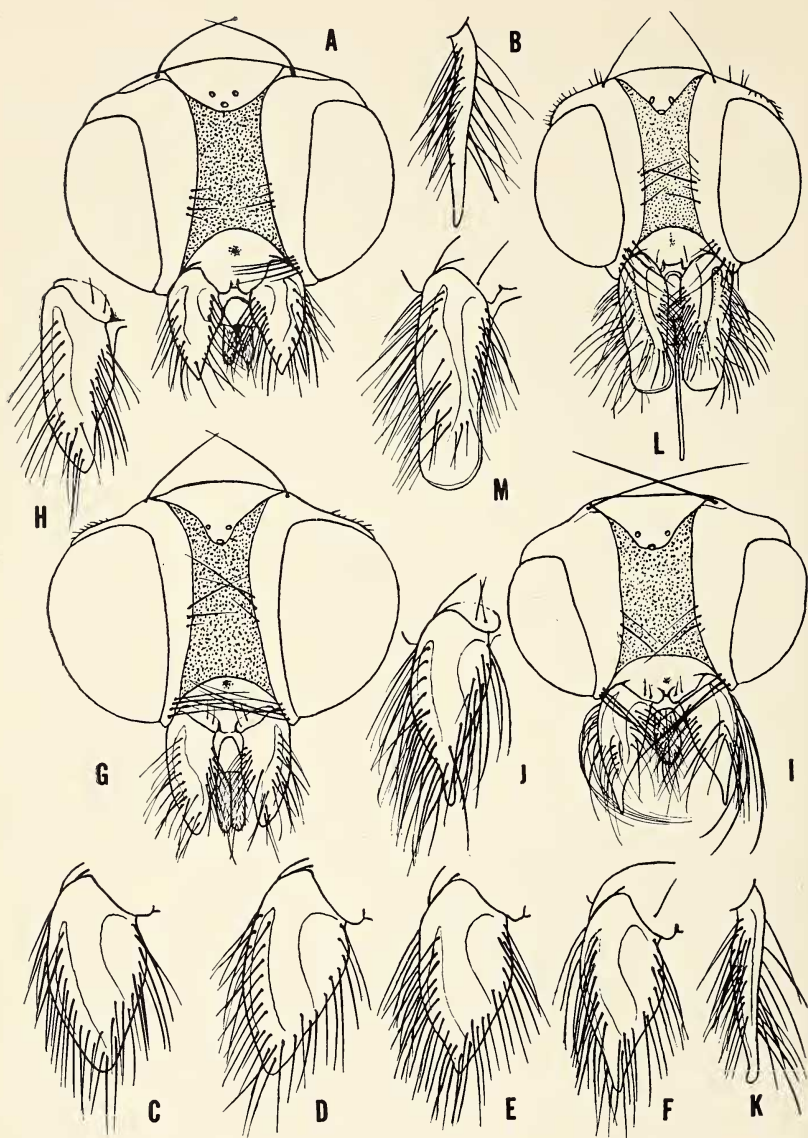


Fig. 43. **A-F**, *Ornithoctona fusciventris* (Wiedemann): **A**, head, ♀, Vermelho, on *Sclerurus s. scansor*; **B** and **F**, side and front views of antennal appendage (2nd segment), ♀, Boquete, on *Pseliophorus tibialis*; **C**, antennal appendage, ♀, Ghost River, on *Vireo philadelphicus*; **D**, same, ♀, Choachi, on *Poecilothraupis igniventris lunulata*; **E**, same, ♀, Falls Church, on *Dendroica tigrina*. **G-H**, *Ornithoctona orizabae* J. Bequaert, ♂ holotype, Orizaba; **G**, head; **H**, antennal appendage. **I-K**, *Ornithoctona oxycera* Falcoz: **I**, head, ♀, El Jonquito; **J**, front view of antennal appendage, ♂, Fusugasugá; **K**, side view of antennal appendage, ♀, El Jonquito. **L-M**, *Ornithoctona (Ornithopertha) nitens* (Bigot), ♀, Turrialba, on *Trogon* sp.: **L**, head; **M**, antennal appendage.

melanoleucus. Holotype in spirit at Paris Mus.; location of pinned paratype unknown). J. Bequaert, 1940, Rev. Acad. Colombiana Cienc. Ex. Fis. Nat., 3, No. 12, p. 416; 1942, Bol. Entom. Venezolana, 1, pt. 4, p. 81. Anduze, Pifano and Vogelsang, 1947, *Op. cit.*, Num. Extra, p. 6.

Distribution and Specimens Examined. COLOMBIA (recorded by Falcoz, 1930): Valdivia, Dept. Antioquia, on *Myiodynastes c. chrysocephalus* (M.A. Carriker, Jr.); Chinchicúa, Sa. Marta, Dept. Magdalena, on *Dendroica striata* and *Turdus olivater sanctae-martae* (M.A. Carriker, Jr.); Fusugasugá, Dept. Cundinamarca, allotype ♂ (Hno. Apolinar-María); Muzo, Dept. Boyaca (Hno. Apolinar-María).

VENEZUELA: El Junquito, 2040 m., near Caracas (P. Anduze); Colonia Tovar, State of Aragua, on *Thraupis cyanocephala olivicyanea* (E. Mondolfi).

This rare Neotropical species is unusual for its restricted distribution, being known only from Colombia and Venezuela.

Known Neotropical Hosts of *O. oxycera* (verified individual records in parentheses): Falconiformes: *Buteo m. melanoleucus*. Passeriformes (4): *Dendroica striata* (1); *Myiodynastes c. chrysocephalus* (1); *Thraupis cyanocephala olivicyanea* (1); *Turdus olivater sanctae-martae* (1).

Bionomics. Nothing is known of the life history of *O. oxycera*. The 5 host records, from as many different species of birds, barely suggest that the only true breeding hosts are most probably Passeriformes.

Affinities. *O. oxycera* is closely related to *O. fusciventris*, from which it differs essentially only in the larger size (nearly 5 mm. in ♀ from tips of antennae to hind margin of scutellum, as compared with about 3.5 mm. for *fusciventris*), and in the antennal appendage being much more slender over the apical half (well beyond the range of variation of *fusciventris*) and distinctly flattened from the sides at the tip (Figs. 43J-K). The head (Fig. 43I) has the sides of the upper orbits more abruptly curved behind than in *fusciventris*, although this feature is exaggerated by Falcoz (1930, p. 37, fig. 1). His drawing of the ♀ abdomen (fig. 3) shows very small 2nd and 3rd median sclerites; but their absolute and relative sizes vary and I have seen some *oxycera* in which they differ scarcely from those of *fusciventris*. The prosternal lobes (Fig. 44E) are longer, straighter and more pointed than in most other *Ornithoctona*, though I have not seen them as slender and sharp as figured by Falcoz (fig. 2). The wing (Fig. 39D) is more extensively covered with microtrichia than in *fusciventris*. Falcoz noted that the apical zone of the basal

abdominal sternite bears crowded small spines; but these are only a little thicker and more spine-like than in other species and are in several irregular rows, not in a true comb.

The allotype of the *male*, here described for the first time, is from Fusugasugá, Colombia, without host (at Mus. Comp. Zool., Cambridge, Mass.). It differs little from the female, except for the usual, large, transverse, median sclerites on the dorsum of the abdomen, which are like those of *fusciventris*. The spine-like setae at the apex of the basal abdominal sternite are longer than in the ♀. The terminalia are similar to those of other *Ornithoctona*. Length from tips of antennae to hind margin of scutellum, 4.5 mm.; of wings, 9 mm.

Original description of *O. oxycera* (translated from the French): "Length, from base of antennae to apex of abdomen, 8 mm. Color uniformly reddish-brown; margins of antennal appendages black. Head $1\frac{1}{2}$ times as wide as long, antennae not included. Clypeus [frons] slightly convex and divided by a shallow longitudinal groove. Orbits widened posteriorly; orbital bristles poorly developed. Occipital triangle or ocellar area [postvertex] twice shorter than wide at base. Frons [mediovortex] a little longer than occipital triangle. Antennal appendages about in sagittal plane of body, lamelliform, twice as long as wide at base, abruptly narrowed at about the apical third, which is drawn out into a point flattened from the sides; dorsal surface with two longitudinal grooves separated by a broad median carina; margins provided with black setae, longer at outer border. Thorax markedly wider than long. Longitudinal suture [median notal suture] very fine; transverse suture evanescent medially. Humeral callosities long and pointed, bearing long setae. Mesothoracic [prothoracic] spiracles oval, very large. Mesopleural setae [on anepisternum] numerous, strong; 2 long prealar setae and 2 prescutellar setae on each side. Scutellum with a transverse groove near hind border, which bears 4 setae. Mesosternal protuberances [prosternal lobes] as in [the author's] fig. 2 [very long, slender and sharp]. Hind legs with a basal comb or etenidium of black spinules on under side of first tarsal segment, as in some other species of the genus. Wings with dark veins; last section of costa a little shorter (for about $\frac{2}{3}$) than penultimate; subcosta ending in costa opposite anterior cross-vein; anterior [first] basal cell a little longer than posterior [second], which is twice as long as anal cell. The areas between cubital [3rd longitudinal] and discoidal [4th longitudinal] and between discoidal and posticalis [5th longitudinal] bear microscopic setulae. Abdomen rather densely covered with black setae, longer along sides and at apex. Dorsally: basal tergite very short, followed by 3 scuta [median sclerites], only the first well developed and rectangular, the others very small and poorly defined; posteriorly, near apex, 2 pregenital protuberances, each with 4 or 5 long setae. Ventrally: basal sternite narrow, rectangular, well sclerotized, bearing at hind margin a kind of etenidium or not very regular row of small black spines. Behind basal sternite, ventral integument with distinct traces of segmentation, 5 sternites being indicated." I have not seen the types, but the description and figures are fully adequate for correct recognition. The author's suggestion that either *O. fusciventris* Wiedemann or *O. nebulosa* Say might have been his *oxycera*, has proved erroneous. Mr. Ségué informs me (*in litt.*, Nov. 1953) that only the holotype, preserved in spirit, is now at the Paris Museum; the pinned paratype is presumably lost.

Subgenus *Ornithopertha* Speiser, 1902

Ornithopertha Speiser, 1902, Zeitschr. Syst. Hym. Dipt., 2, p. 167 (monotypic for *Ornithomyia nitens* Bigot, 1885).

Antennal appendage about three times as long as its greatest width, the tip very broad and evenly rounded, the outer and inner margins parallel, the upper surface grooved lengthwise.

Speiser's original diagnosis was as follows (translated from the German): "Antennal appendages more than twice as long as wide and two-thirds of the length of the head. Scutellum appearing very slightly swollen, in any case uniformly convex and without median longitudinal depression. Legs, wings, abdomen and shape as in *Ornithoctona*, except for the strikingly aberrant head." I have omitted from my own definition the character taken from the scutellum, which is at best of specific value only. Some species of *Ornithoctona*, proper, lack all indication of a longitudinal depression. Moreover, Speiser himself later described the scutellum of his *Ornithopertha anthracina* (a synonym of *O. nitens* in my opinion) as having a fine median furrow over about three-fifths of the length.

Ornithoctona (Ornithopertha) nitens (Bigot)

Figs. 39E, 43L-M, and 44A

- Ornithomyia nitens* Bigot, 1885, Ann. Soc. Ent. France, (6), 5, p. 241 (no sex; no host. Panama. Types ♀ from the Bigot collection, now in the J.E. Collin collection at Newmarket, England).
- Ornithopertha nitens* Speiser, 1902, Zeitschr. Syst. Hym. Dipt., 2, p. 166 (types). Aldrich, 1902, Smithson. Misc. Coll., 46, No. 1444, p. 657. Speiser, 1904, Ann. Mus. Nat. Hungarici, 2, p. 393 (types); 1907, Ent. News, 18, p. 103; 1908, Zeitschr. Wiss. Insektenbiol., 4, p. 304. Lutz, Neiva and da Costa Lima, 1915, Mem. Inst. Osw. Cruz, 7, p. 192 (copy of description). Bau, 1929, Zoolog. Anzeiger, 85, p. 10. J. Bequaert, 1940, Rev. Acad. Colombiana Cienc. Ex. Fis. Nat., 3, No. 12, p. 416; 1942, Bol. Entom. Venezolana, 1, pt. 4, p. 81. Anduze, Pifano and Vogelsang, 1947, *Op. cit.*, Num. Extra, p. 6.
- Ornithomyia geniculata* Bigot, 1892, The Humming Bird, 2, p. 49 ("♀ ♂"). Costa Rica: on *Pharomachrus mocino costaricensis*. Types ♀ from the Bigot collection, now in the J.E. Collin collection at Newmarket, England).
- Ornithopertha geniculata* Speiser, 1904, Ann. Mus. Nat. Hungarici, 2, p. 394 (types); 1907, Ent. News, 18, p. 103. Aldrich, 1907, Jl. New York Ent. Soc., 15, p. 6. Speiser, 1908, Zeitschr. Wiss. Insektenbiol., 4, p. 304. Bau, 1929, Zoolog. Anzeiger, 85, p. 10 (specimens without locality).
- Ornithopertha anthracina* Speiser, 1904, Ann. Mus. Nat. Hungarici, 2, p. 393 (no sex; no host. Honduras. Type in Vienna Mus.); 1907, Ent. News, 18, p. 103; 1908, Zeitschr. Wiss. Insektenbiol., 4, p. 304. Bau, 1929, Zoolog. Anzeiger, 85, p. 10 (Venezuela).
- Ornithomyia erythrocephala* Howard, 1902, The Insect Book, Pl. 22, fig. 3^a Not of Leach, 1817.

Distribution and Specimens Examined. MEXICO: El Ocote, Ocozocoautla, 650 m., State of Chiapas, 1 ♀ on *Trogon m. massena* (Miguel Alvarez del Toro); Santa Rosa, Comitán, State of Chiapas, 3 ♀ on *Pharomachrus m. mocino*, *Oreopeleia m. montana* and *Trogon collaris puella* (Esc.N.C.Biol., México).

REPUBLIC OF HONDURAS (recorded by Speiser, 1904, as *anthracina*): Portillo Grande, Dept. Yoro, 5000 ft., 1 ♀ on "quetzal," *Pharomachrus m. mocino* (R.E. Stadelman).

NICARAGUA: San Ramón, 1 ♀ on *Phaethornis superciliosus longirostris*.

COSTA RICA (recorded by Bigot, 1892, as *geniculata*): without precise locality, on *Pharomachrus mocino costaricensis* (A. Boucard. — 3 ♀ cotypes of *O. geniculata* Bigot), and without host, 1 ♀ (Univ. Minnesota) and 2 ♀ (José C. Zeledon. — Specimen at U.S.Nat.Mus. figured by Howard, 1902, as *Ornithomyia erythrocephala*); Volcán Turrialba, 1800 ft., 1 ♀ on *Trogon* sp. (Am.Mus.N.H.).

PANAMA (recorded by Bigot, 1885): without precise locality or host (4 ♀ cotypes of *O. nitens*); El Volcán, Chiriqui Prov., 1 ♀ on *Trogon* sp. (C.B. Worth); Barriles, a few miles W. of El Volcán, Chiriqui Prov., 1 ♀ on *Trogon collaris puella* and 1 ♀ on *Troglodytes musculus inquietus* (Mrs. M.E. McLellan Davidson).

COLOMBIA: Sierra del Líbano, Santa Marta, 6000 ft., Depto. Magdalena, 2 ♀ (H.H. Smith); Chinchicúa, Santa Marta, Depto. Magdalena, 1 ♀ on *Trogon p. personatus* (M.A. Carriker, Jr.).

VENEZUELA (recorded by Bau, 1929, as *anthracina*): Mérida, 1 ♀ (S. Briceño).

O. nitens is strictly Neotropical, being known thus far from southern Mexico (Chiapas) to Colombia and Venezuela.

Known Neotropical Hosts of *O. nitens* (verified individual records in parentheses). Columbiformes (1): *Oreopeleia m. montana* (1). Apodiformes (1): *Phaethornis superciliosus longirostris* (1). Trogoniformes (9): *Pharomachrus m. mocino* (2); *P. mocino costaricensis* (1); *Trogon* sp. (2); *T. collaris puella* (2); *T. m. massena* (1); *T. p. personatus* (1). Passeriformes (1): *Troglodytes musculus inquietus* (1).

Bionomics. The recorded captures, though few, seem to be satisfactory evidence that trogons (Trogoniformes) are the true and possibly sole breeding hosts of *O. nitens*. Of the 12 verified records 9 are from trogons; the remaining 3, from a pigeon (*Oreopeleia*), a hummingbird (*Phaethornis*) and a wren (*Troglodytes*), are either accidental occurrences or perhaps unreliable.

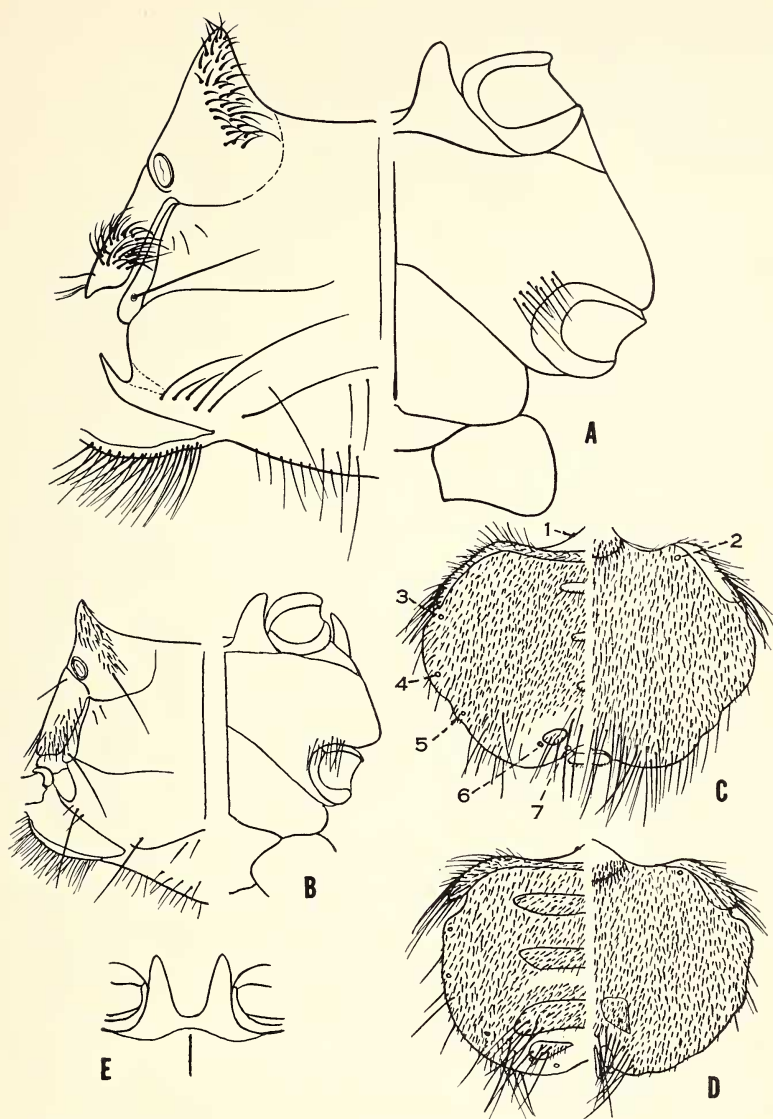


Fig. 44. **A**, *Ornithoctona* (*Ornithopertha*) *nitens* (Bigot), thorax dorsally and ventrally, ♀, Turrialba, on *Trogon* sp. **B**, *Ornithoctona orizabae* J. Bequaert, thorax dorsally and ventrally, ♂ holotype, Orizaba. **C**, *Ornithoctona fusciventris* (Wiedemann), abdomen dorsally and ventrally, ♀, New York; spiracles numbered 1 to 7. **D**, *Ornithoctona erythrocephala* (Leach), abdomen dorsally and ventrally, ♂, Orient, on *Accipiter striatus velox*. **E**, *Ornithoctona oxycera* Falcoz, prosternal lobes, ♀, Chinchicúa, on *Turdus olivater sanctae-martae*.

The puparium and other details of the life-history are unknown.

Affinities. *O. nitens* occupies an isolated position in the genus. The legs of the female I have seen from Turrialba, Costa Rica, were dull grass-green, showing that the haemolymph may contain green pigment, as in other species of *Ornithoctona*.

Speiser accepted 3 species of *Ornithopertha*, based on color differences; but I recognize only one. Although he had originally failed to distinguish the types of *geniculata* from those of *nitens*, he later attempted to separate these two forms as follows, while admitting that they might be only extremes of a "chain of variations" ("Variationsreihe"):

1. Sternum uniformly yellow or at least without well-defined dark nut-brown spots before the mid coxae *O. geniculata*
 Sternum with a large, somewhat triangular dark nut-brown spot on each side between the fore and mid coxa *O. nitens*

Speiser himself stated that, of Bigot's 4 cotypes of *nitens*, 3 had the sternal dark spots, while in the fourth the sternum was entirely yellow; on the other hand, of the 3 cotypes of *geniculata*, 2 had the sternum only very slightly darkened, but the third had it distinctly spotted. His *O. anthracina*, discussed later in detail, was based also chiefly on color, particularly on the brownish pitch-black head and thorax. A study of 23 specimens shows that these color differences are wholly unreliable, varying individually, the extremes being connected by transitions.

The male of *O. nitens* is as yet unknown. The cotype of *geniculata* which Bigot described as the male is a female, so far as could be determined.

In addition to the characters mentioned in the key, the species is remarkable in the genus *Ornithoctona* for its extreme hirsuteness, caused more by the unusual length and thickness of the setae than by their increased number. The bristles are particularly strong on the antennal appendages, under side of head, humeral callosities, anepisternum, axillary cord, tegula, and basal section of costa. There is only one notopleural bristle. The preäpical scutellar setae are very weak and few, 6 to 8 on each side placed in one irregular, transverse row and some longer than others; the base of the scutellum also bears a few weak setae. Three to 6 strong, but rather short vertical bristles form a group near each outer corner of the post-vertex; but the orbital bristles at mid-height of the face are not more numerous than usual in *Ornithoctona* (3 or 4). Both dorsally and ventrally, the abdomen is mostly covered with very long, ap-

pressed setae, giving it a fuzzy appearance. On the legs also the setae are very long and thick, though not much more numerous than usual; they tend to form tufts near the tips of the femora. The transverse comb of stiff setae on the under side of the hind basitarsus is strikingly developed. The setae near the apical margin of the basal abdominal sternite, on the other hand, are few and very weak, hair-like.

Original description of *O. nitens* (French text translated): "Long, 9 mm. Nitida. Antennis nigris nigroque villosis; palpis flavidis; fronte testacea; oculis nigris; thorace nigro, linea media angusta, fulvida, humeris late, scutello, testaceis; abdomine nigro fusco, breviter et parce piloso; pedibus flavide lividis, geniculis, linea tibiarum laterali angusta, tarsis, omnino, fuscis; alis pallide fuscis, venis, costali, longitudinalibus, 1-4is omnino, nigris, 5a et 6a, parum ultra transversas, ejusdem coloris, istis in medio pallidis.—Very shiny. Antennae testaceous, with black hairs; palpi yellowish; eyes black; frons [interocular face] yellowish; ocelliferous spot [postvertex] black; thorax yellowish, the dorsum broadly black, with a very narrow, reddish median line; humeral callosities broadly and scutellum testaceous, the latter with several blackish setae in the middle; sternum testaceous, with two large, blackish lateral spots; abdomen pale brown or yellowish, with scattered black hairs; legs pale yellowish, with knees, tarsi and a narrow margin along outer face of hind tibiae blackish; wings russet, veins brownish; costa, 1st to 4th longitudinals entirely, and 5th and 6th longitudinals to a little beyond 1st cross-vein, black, all of the same black color, the 2nd cross-vein brown; 1st longitudinal ending in costa about opposite the 1st (or outer) cross-vein, 2nd ending opposite 2nd cross-vein, and 3rd ending rather close to tip of 4th longitudinal; 2 basal cells fairly unequal." The five specimens mentioned by Bigot are now the property of Mr. J.E. Collin, in whose collection I have recently (1951) studied them. As Speiser (1902) recognized, four of them are cotypes of *nitens* and the fifth is a male of *Ornithoetona erythrocephala* (Leach) (= *haitiensis* Bigot). Speiser added the following information on the structural characters: "Vertex evenly rounded; postvertex wider than long; interocular face ["Stirn"] parallel-sided, with a dull median field [mediovortex] which widens somewhat anteriorly beyond mid-length. Clypeus [interantennal frons] very short, with a symmetrical pair of notches at anterior margin. Antennal appendages long and not pointed as in the other species of *Ornithoetona*, but ending very broadly and bluntly. Thorax with a fine longitudinal line [median notal suture] and a transverse [mesonotal] suture blurred in the center; scutellum shaped as described in the generic diagnosis of *Ornithopertha*. The color is given correctly by Bigot. The fore legs lack the plate-like apical spine of the tibiae, present in the related Indo-Australian species [*Ornithoetona plicata* (v. Olfers)]. Shape and venation of wings do not differ essentially from those of *Ornithoetona*. The 1st longitudinal vein ["Subcostalis"] ends either before or just opposite anterior cross-vein ["kleine Querader"]; the 2nd longitudinal ["Radialis"] ends so close to 3rd ["Cubitalis"], that the last section of costa is only half as long as the penultimate. The 2nd basal cell ["hintere Basalzelle"] is shorter than 1st ["vordere Basalzelle"] only to the extent of the length of anterior basal cross-vein ["hintere Querader"]; it is much wider than the 1st, the anterior basal cross-vein being a little over twice the length of anterior cross-vein. Anal cell less than half the length of 2nd basal cell. Alula ["Anallappen"] of the wing distinct." Speiser's diagnosis of his genus *Ornithopertha* states also that the scutellum appears to be very slightly swollen, at any rate evenly convex, and without longitudinal median depression. All four cotypes of *O. nitens* appear to be females.

Original description of *O. geniculata* (French text translated): "Long. ♂ 9, ♀ 10 mm. ♂ Haustello palpisque fulvis, antennis, ejusdem coloris, nigro setosis, oculis fulvis, late nigro notatis, capite fulvo, facie utrinque carinata, tergo nigro nitido, antice, utrinque, macula lata, quadrata flava, lineaque angusta fulva, mediana, pectis; scutello flavido, nigro setoso; pectore flavido; abdomine obscure-fusco sat dense nigro velutino: pedibus pallide fulvis, nigro parce setosis, geniculis nigris; alis pallidissime fulvidis, venis nigris, transversa interna pallida. ♀ Paulo majore, abdomine, latiore, bilobato, oculis omnino fulvis, scutello fusco nigro, et nigro setoso.—♂ Proboscis and palpi fulvous; antennae fulvous with black setae; head fulvous; face with two strong lateral and longitudinal carinae; eyes fulvous with a large and long black spot; dorsum shiny, black anteriorly; on each side a large yellowish quadrangular spot and in the middle a fine, median, longitudinal yellowish line; scutellum yellowish, with scattered black setae; pleura and sternum fulvous; abdomen blackish-brown, covered rather densely with very short brown hairs; legs pale fulvous-yellow, with some sparsely scattered black setae; knees black; tarsi at their apices with many short, black setae; wings very pale brownish; veins blackish, except inner cross-vein which is pale yellowish-white.—♀ Size somewhat larger; abdomen broad, bilobed; eyes uniformly fulvous; scutellum shiny black." All 3 cotypes, which I have recently (1951) studied in Mr. J.E. Collin's collection, appear to be ♀, not 2♂ and 1♀ as Bigot thought. Speiser (1902b, p. 167) at first did not recognize them as the types of *geniculata*, since he listed them as additional specimens of *O. nitens*, although one bears Bigot's original label "*geniculata*", as well as the mention of the host. When his attention was later called to the fact, Speiser attempted to separate *geniculata* as a distinct species, on the basis of certain color differences (1904d, p. 394); but, as shown above, these are unreliable. A most careful comparison has failed to disclose structural differences between the cotypes of *nitens* and those of *geniculata*.

Original description of *O. anthracina* (translated from the German): "Length, 9.5 mm.; from oral margin to hind margin of scutellum, 4.75 mm. General color shiny, somewhat brownish pitch-black; only head beneath pale, almost whitish yellow, and anterior or upper surface of tibiae paler in the middle than the edges, brownish-yellow; tips of antennal appendages also translucent brown. Structure of head not differing from that of *O. nitens* Big.; post-vertex insignificantly narrower in proportion to its length and median dull area of vertex [mediovertex] even less widened anteriorly than in that species. Pre-scutum and scutum of mesothorax, as well as sternum, without peculiarities beyond the different color; but scutellum with a fine median furrow, extending behind over only about $\frac{2}{3}$ of the length, where it stops. Abdomen and legs showing nothing special. Wings darker than in *O. nitens*, umber-brown; venation exactly as in that species." I have not seen the type of *anthracina*; but, except for the presence of the fine furrow over part of the scutellum, the description mentions only color differences, which I cannot regard as reliable for specific distinction. Of two ♀ taken together in the Sierra del Líbano, Colombia, one has head and thorax almost entirely black, as Speiser described for his *anthracina*; while the other has the whole of head and thorax very extensively yellowish-brown; yet no structural difference could be detected. I can only consider *anthracina* as a synonym of *nitens*.

(To be continued in vol. XXXV)